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Factors Affecting Recovery from Defoliation during Drought in Two Aridland Tussock Grasses

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FACTORS AFFECTING RECOVERY FROM DEFOLIATION DURING DROUGHT IN TWO ARIDLAND TUSSOCK GRASSES

by

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ABSTRACT

Factors Affecting Recovery from Defoliation during Drought in Two Aridland Tussock Grasses

by

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The importance of several factors in limiting recovery from defoliation was investigated in field-grown plants of Agropyron desertorum and Agropyron spicatum exposed to drought , natural or irrigated conditions. Leaf extension rate, components of leaf area production, number of metabolically active axillary buds and carbohydrate availability were examined on the same plants immediately after defoliation and/or in the following spring from 1984 until 1986.

The diurnal course of leaf growth did not relate to turgor pressure in the expanded portion of leaf laminae. Rather growth was apparently associated with air temperature. Leaf extension rate was lower under drought than under better moisture levels during 1984 to 1986. For both species, reduced growth rates and shorter growth periods resulted in reduced tiller height, leaf number and

leaf size under drought compared with natural or irrigated conditions in 1985 and 1986, but not in 1984. As a result, leaf area and/or yields were also lower under drought in 1985 and 1986, and lowest under drought plus defoliation in 1986. Production of daughter tillers immediately after defoliation was also lowest under drought.

Regrowth capacity of both species was not limited by axillary bud number, size or viability immediately after defoliation under any water level in 1986. In early spring, however, tiller number and growth were lower on clipped than on unclipped plants of both species under drought and irrigated conditions in 1986, and under all water levels in 1987; this resulted in considerably reduced photosynthetic canopies on clipped plants.

Crown and root total nonstructural carbohydrate (TNC) pools were higher under drought than under better moisture levels in A. desertorum and A. spicatum in early spring 1986. These high pools of TNC apparently enhanced the production of etiolated regrowth in both species when meristematic limitations did not exist in early spring.

The productive potential of both Agropyron species will probably not be affected following a late and severe defoliation under drought. However, vegetative growth and/or productivity, and probably the persistence of these species in the community, will be reduced after two or more years of late and heavy defoliations under drought.

(159 pages)

CHAPTER I

INTRODUCTION

Rapid regrowth following defoliation is important if plants are to tolerate herbivory with minimal damage. High growth rates after defoliation could allow plants to more rapidly reestablish the root/shoot balance and to obtain a greater share of the available space and the resources included in that space thereby better maintaining their competitive position in relation to their neighbors. Following defoliation, rapid production of new leaves on remaining shoots with intact apical meristems and/or activation and growth of axillary buds into tillers could also add to perennation by the addition of axillary buds to the tussock's bud bank.

Immediately after defoliation, grasses can reestablish a photosynthetic canopy by producing both leaf blades and leaf sheaths. These may grow from either undefoliated or defoliated shoots with intact intercalary and apical meristems. They may also be produced from the growth of axillary buds into new shoots. Therefore, any stress, such as drought, which reduces leaf extension, tiller production and growth, or axillary bud production, activity or viability could impose a limitation on the regrowth potential of a particular species.

Range grasses are commonly defoliated under water deficit conditions in arid and semiarid areas (Ludlow,

1986). The interaction of drought and defoliation may reduce plant survival. This response has been observed when pastures have been defoliated during natural droughts (McLean and Ryswyk, 1973; Breman and Cissé, 1977; Ganskopp and Bedell, 1981; Currie and White, 1982). Most of these studies, however, have limited value for understanding the mechanisms of plant response to the combination of drought and defoliation since predetermined levels of defoliation or drought stress and/or control plants were not measured. A few investigations (e.g. Sosebee and Wiebe, 1971; Mohammad et al.,1982) have observed responses to the simultaneous imposition of both stresses, but most of these studies have been conducted under either greenhouse or growth chamber conditions. These results cannot be applied directly to rangelands because plant responses differ substantially between the field and controlled environments, especially with regard to water stress (Ludlow and Ng, 1976; Bunce, 1977; Turner and Begg, 1978).

Two important tussock grasses, Agropyron spicatum (Pursh) Scribn. and Smith* and Agropyron desertorum (Fisch. ex Link) Schult., were utilized in this study of the interaction of drought and defoliation. A. spicatum is a

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* A name change to Pseudoroegneria spicata (Pursh) A. Löve ssp. spicata has been recommended by Barkworth and Dewey (1985).

native codominant grass species and an important component on 44.8 million hectares of sagebrush/bunchgrass rangeland in the Intermountain West of the U.S.A. (West, 1983). A. desertorum, introduced from Eurasia (Dewey and Asay, 1975), is ecologically well-adapted to much of western North America. This species grows on more than 5 million hectares in the United States (Dewey and Asay, 1975). These two grasses are very similar in physiological, morphological and phenological characteristics (Caldwell et al., 1981; Nowak and Caldwell, 1984). A. desertorum is, however, more tolerant of grazing than A. spicatum (Hyder and Sneva, 1963; Caldwell et al., 1981). To closely simulate rangeland conditions, the experiments were conducted in field plots with interspersed and non-defoliated plants of Artemisia tridentata ssp. vaseyana (Rydb.) Beetle. Similar, adjacent plots were exposed to drought, natural precipitation or irrigated conditions. Levels of both water stress and defoliation were determined.

Effects of defoliation or drought on factors that may be important determinants of plant regrowth, i.e. leaf extension rate; tillering and components of leaf area production; number, activity or viability of axillary buds; and carbohydrate availability, are briefly reviewed here. Then, the main objectives of this study and the organization of the dissertation are described.

Effects of Defoliation

After grazing, leaf growth can be rapid from intact intercalary and apical meristems on defoliated or undefoliated shoots. Among graminoids leaf extension rates immediately following clipping or grazing may be greater than (McNaughton, 1979, 1983; Wolf and Parrish, 1982; Wallace et al. ,1985; Olson and Richards, 1988a) or less than (Toft et al., 1987; Olson and Richards, 1988a) those on undefoliated controls.

When clipping or grazing removes existing active meristematic tissues, a new photosynthetic canopy can only be reestablished through the production of new tillers from axillary buds (Hyder, 1972; Jewiss, 1972). Intensive and frequent clippings during one or more years have lowered tiller production in several grass species (Neiland and Curtis, 1956; Stout et al., 1980, 1981; Hall et al., 1987; Olson and Richards, 1988b). Inhibitory effects that defoliation may have on bud outgrowth (Mitchell, 1953) or on survival of new tillers (Olson and Richards, 1988b) could explain this plant response.

The ability to quickly reestablish a photosynthetic canopy may vary among species. For example, the capacity to rapidly form new tillers and allocate carbon resources to shoot regrowth is greater in A. desertorum than in A. spicatum (Caldwell et al., 1981; Richards, 1984; Richards and Caldwell, 1985).

Another factor that may affect regrowth of grasses is non-structural carbohydrate availability. Some studies (e.g., McIlvanie, 1942; Trlica and Cook, 1972; Daer and Willard, 1981) suggest that reserve carbohydrates have a dominant and fundamental role in plant regrowth. Other studies (e.g., Davidson and Milthorpe, 1966; Richards and Caldwell, 1985; Richards, 1986; Thorgeirsson, 1988), however, have demonstrated that reserve pools might be better perceived as buffers rather than reservoirs, and that morphological and developmental characteristics may limit regrowth to a greater extent than the availability of carbon reserves. Nevertheless, soluble carbohydrates are clearly important at least in initiating regrowth (Heilmeier et al., 1986) when the photosynthetic surface area is nonexistent or inadequate to maintain both respiration and growth demands. Soluble carbohydrate availability is probably most important when morphological-developmental constraints are not limiting. The effects of clipping or grazing on crown and root carbohydrate levels of grasses are also contradictory. Clipping or grazing could diminish (Cook et al., 1958; Buwai and Trlica, 1977a) or not affect (Jameson and Huss, 1959; Buwai and Trlica, 1977a; Menke and Trlica, 1983) carbohydrate concentrations in crowns or roots. Similarly, carbohydrate pools may decrease (Humphreys and Robinson, 1966; Caldwell et al., 1981) or stay the same (Buwai and Trlica, 1977b; Christiansen and Svejcar, 1987) after

defoliation.

Effects of Drought

Leaf extension and tiller expansion are very sensitive to water deficits largely because of the requirement of turgor for cell expansion (i.e., Boyer, 1968; Squire et al., 1983; Ong et al., 1985). The more severe the water stress conditions, the lower the leaf extension rate (i.e., Boyer, 1970; Hsiao, 1973; Hsiao et al., 1985). However, water potential (Hsiao et al., 1970; Westgate and Boyer, 1985), cell wall extensibility (Davies and Van Volkenburgh, 1983; Van Volkenburgh et al., 1985b) and the difference between the xylem water potential and the water potential of the extending tissue (Boyer et al., 1985) are also sensitive to water stress and may thus affect growth rate.

Lower growth rates under water stress will ultimately affect many plant morphological characteristics. For example, leaf number (Karamanos, 1978), size (Acevedo et al.,1971; McCree and Davis, 1974; Bunce, 1977) and production rate (Norris, 1982, 1985; Chapman et al., 1983; Ong et al., 1985), plant height (Denmead and Shaw, 1960; Stout et al., 1978; Chung and Trlica, 1980; Turner et al., 1986) and leaf area (Lawlor and Milford, 1973; Takami et al., 1982; Rozijn and Van der Werf, 1986; Sobrado, 1986; Bittman and Simpson, 1987) are all reduced by water deficits. In addition, water stress commonly hastens plant

senescence (Finch-Savage and Elston, 1976; Karamanos, 1978; Dwyer and Stewart, 1987).

After foliage senescence in perennial grasses at the end of the growing season, new photosynthetic tissue is usually produced from the outgrowth of axillary buds. The differentiation and development of axillary buds, however, may be retarded or stopped by water deficit in range grasses (Olmsted, 1941). Water stress is also important in regulating bud activity of several grass species (Gardner, 1942; McIntyre, 1976; Klepper et al., 1982; Nus and Hodges, 1986). Retardation or stoppage of bud growth by low humidity could be a direct response to a decreased hydration of tissues (McIntyre, 1976).

Low water supply also tends to cause a carbohydrate build-up in plant tissues (Allsopp, 1964; Brown and Blaser, 1965; Blaser et al., 1966; Whalley and Davidson, 1969) because water stress restricts growth relatively more than photosynthesis (Wardlaw, 1969; Boyer, 1970; Hsiao, 1973). A greater carbohydrate concentration in developing plant organs might promote increased tissue differentiation (Allsopp, 1964). Carbohydrate concentrations, however, are unlikely to be directly involved in the control of bud development (McIntyre, 1967), rather they might determine the synthesis of other substances more specific in their morphogenetic effects. Increased tillering has been associated with high levels of carbohydrate reserves on

grass plants with different amounts of residual leaf area after defoliation (Ward and Blaser, 1961; Humphreys and Robinson, 1966). However, tiller appearance is the result of complex and dynamic interrelationships between environmental and biological variables (Mitchell, 1953; Auda et al., 1966; Jewiss, 1972; Fletcher and Dale, 1974; Woodward and Marshall, 1988). Thus a positive relationship between tillering rate and carbohydrate availability may not always be found (i.e., Auda et al., 1966; Richards et al., 1988).

Objectives

In this study, several important factors which could limit recovery from defoliation during one or more years of experimentally-imposed drought were investigated on field-grown plants of A. desertorum and A. spicatum. Two periods of growth were examined: (1) regrowth immediately after defoliation during drought and (2) growth in the following spring. Thus this study had two main objectives. The first objective sought to determine if leaf extension rates, tillering and components of leaf area production and/or the number of metabolically active axillary buds were important in limiting rapid regrowth on both species immediately after defoliation during drought. The second objective was to determine if the number of metabolically active axillary buds, determinants of leaf area production and/or crown and root carbohydrates could impose a constraint in the initial

spring growth of these species after they had been defoliated under drought during one or more preceding growing seasons.

The study site and treatments utilized in this investigation are described in Chapter II. Immediate reestablishment of green tissue following defoliation is characteristic of plants tolerant of grazing. Rapid regrowth, however, may become limited under drought conditions because of the effects of water stress on the rate of leaf extension. Effects of drought and of drought and defoliation on leaf extension rate of A. desertorum and A. spicatum are reported in Chapter III; the diurnal course of leaf growth in both species and its relation to leaf water status and air temperature are also presented in this chapter. In addition to the rate of leaf extension, morphological characteristics such as number of green leaves and size of these leaves (length and width of blades and stem + sheaths), tiller height and production of new tillers are also important determinants of regrowth production. The effect of drought or the interaction of drought and defoliation on these components is the subject of Chapter IV. If grazing removes active meristematic tissues, however, regrowth of foliage must depend on growth of axillary buds into tillers. Thus if drought or drought and defoliation reduce axillary bud number, activity or viability, regrowth capacity may then become severely limited (Chapter V).

Following spring defoliation, regrowth may not occur under drought conditions (Cook and Stoddart, 1953; Roundy et al., 1985) or after a severe and late clipping (Wilson et al., 1966; Olson and Richards, 1988a) in Agropyron desertorum and Agropyron spicatum. Tillering of these species, however, would normally occur after rains in the following late-summer or fall (Mueller and Richards, 1986). However, if these species receive limited autumn moisture, tillering could not take place. Under these conditions the axillary buds produced before defoliation in that year will constitute the bud pool for growth in the following spring. Outgrowth of these buds into tillers in early spring, however, could be severely limited if their metabolic activity was reduced by drought or defoliation during drought in the preceding year (Chapter V). The reestablishment of a green canopy could be reduced even further if growth of spring-produced tillers is constrained by drought in that spring (Chapter IV). Also, the availability of carbon reserves in storage organs could influence the rate and amount of growth produced in early spring (Chapter VI). The combined influence of the rate of leaf extension, tillering and components of leaf area production, number of metabolically active axillary buds and carbohydrate availability as determinants of recovery from defoliation during drought is summarized in Chapter VII.

CHAPTER II

STUDY SITE AND TREATMENTS

Study Area and Plant Materials

This research was conducted from 1984 to 1986 at a site typical of Intermountain cold-desert shrub steppe vegetation (West, 1983) located 4 km northeast of Logan, Utah (41° 45'N, 111° 48'W, 1460 m a.s.l.). In 1978, A. desertorum and A. spicatum were established in cleared, but not plowed, 8 m x 8 m plots in a matrix (50 cm x 50 cm) of alternating grass and mountain big sagebrush (Artemisia tridentata ssp. vaseyana (Rydb.) Beetle) transplants such that each grass plant was surrounded by four sagebrush plants. A. tridentata was included in the experimental plots because this species is a natural competitor of both Agropyron species in the rangelands of the Intermountain West. Including this competitor makes the results of this common garden study more realistic than could be obtained with widely spaced plants or conspecific neighbors only. More realistic defoliation responses were expected because regrowth in A. spicatum (Mueggler, 1972) and tiller replacement of clipped tillers in A. desertorum (Olson, 1986) can be reduced by the presence of undefoliated neighbors. A. spicatum and sagebrush transplants were obtained from native populations at the study site and A. desertorum transplants were collected in seeded pastures in central Utah. Each plot contained 289 plants of which 25 % were A. desertorum and

25 % were A. spicatum.

The mean air temperatures from May to July were 16.8 C in 1984, 18.4 C in 1985 and 17.4 C in 1986. Further details of the site and long-term climate information are given in Caldwell et al. (1981).

Experimental Treatments

Plant responses were assessed on clipped or unclipped plants of both grass species under drought, natural or irrigated conditions. There was one plot for the drought treatment and 2 replicate plots each for the natural and irrigated water levels.

Clipping Treatments

In each plot, half of the grasses were clipped while the other half remained unclipped. Plants of both bunchgrass species were defoliated once each year to a 5 to 7 cm stubble height during May or June of 1984, 1985 and 1986. This intensity (approximately 85 % green foliage removal) and timing of defoliation simulated normal spring grazing by livestock (Norton and Johnson, 1983; Olson and Richards, 1988a).

Water Levels

A rainout shelter was used to impose the drought treatment (Arkin et al., 1976). It automatically covered the drought plot during precipitation events during the growing

seasons of 1984, 1985 and 1986. This plot, however, received some water during the 1984 growing season, in fall 1983 and 1984, and in late winter-early spring 1986 (Fig. 1). The natural plot received naturally occurring rain or snow. Drip irrigation (about 20 mm d^{-1} during the study periods) was used to obtain the irrigated water level.

Precipitation events were monitored by a micrometeorological station located at the site. Amounts of precipitation (October-September) allowed on the drought plot were 180, 158 and 149 mm during 1983/4, 1984/5 and 1985/6, respectively. The natural plot received 737, 526 and 824 mm and the irrigated plot 1816, 2118 and 3157 mm, respectively. Normal precipitation (223 mm) was allowed on all 3 plots from October 1986 until mid-May 1987, when final measurements of bud metabolic activity (Chapter V) were completed.

Soil Water Status

Soil water potential was measured in each water-regime plot every 10 to 15 days in 1984, 1985 and 1986 using thermocouple psychrometers at depths of 10, 20, 35, 50 and 80 cm (see Fig. 24 in Appendix). During the study periods, soil water potentials averaged over all depths (Fig. 1) were generally less than one-half as stressful in the irrigated than in the drought treatment. The rate of development of soil water deficits in the drought plot in 1984, 1985 and 1986 (> -0.03 MPa d^{-1}) was comparable to that reported in

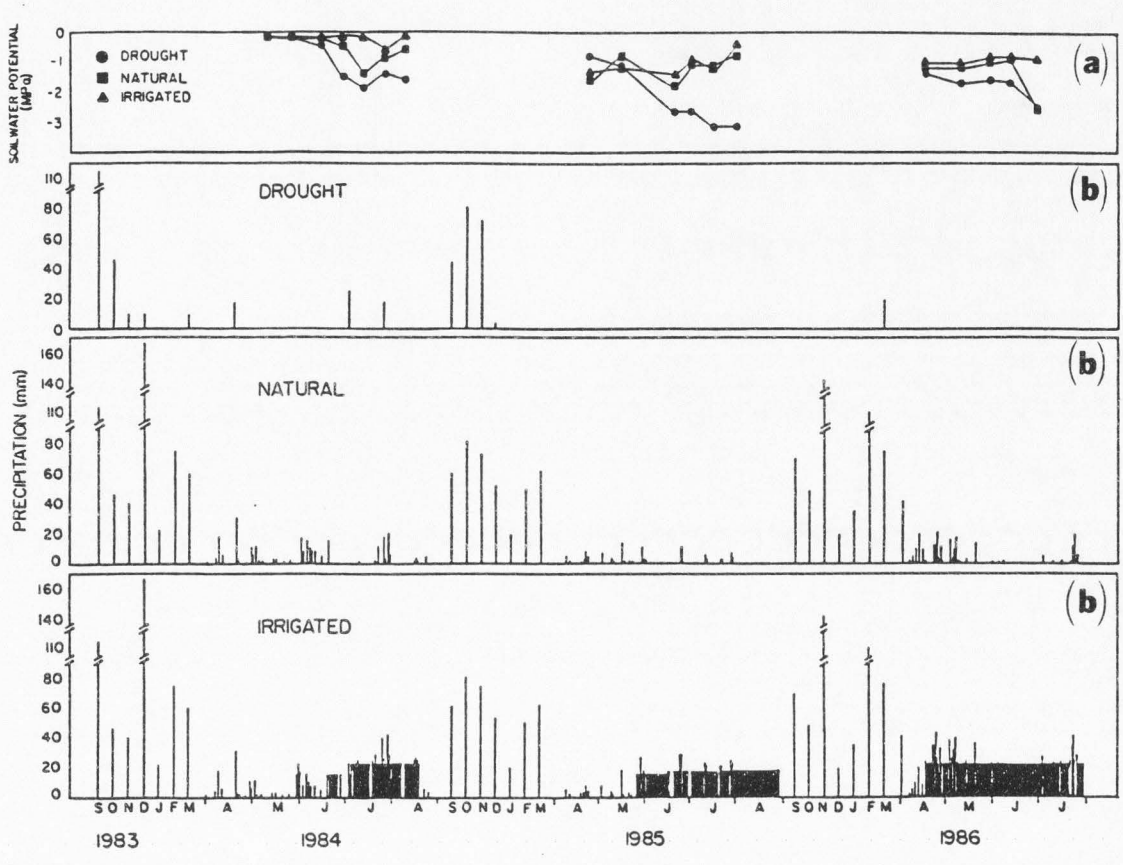


Fig. 1. (a) Soil water potentials averaged over all measured depths (10, 20, 35, 50 and 80 cm) in the drought, natural and irrigated plots during the growing seasons of 1984, 1985 and 1986. Each symbol is the mean of 3 or 4 psychrometer observations. (b) Seasonal distribution of precipitation events on the drought, natural and irrigated plots from September 1983 until July 1986. The blackened areas represent water added by drip-irrigation (approximately 20 mm d^{-1}).

other field studies (i.e., Fereres *et al.*, 1978; Keatinge *et al.*, 1979). The natural plot had soil water potentials similar to or slightly lower than those observed in the irrigated plot, where values were usually greater than or equal to -1.0 MPa at all depths.

Plant Water Status

Predawn and midday xylem pressure potentials were determined every 10 to 15 days with a pressure chamber (Waring and Cleary, 1967); youngest fully expanded leaves were sampled for these measurements. Tissue water loss between sampling and measurement was minimized by enclosing the sampled plant material in a plastic bag (Turner, 1981).

Predawn leaf xylem pressure potentials were lower in the drought plot than in the other plots for both species (Fig. 2). Midday xylem pressure potentials were on average > 0.55 MPa lower than those at predawn in 1984 to 1986. Predawn leaf water potentials in *A. desertorum* and *A. spicatum* exposed to the drought treatment declined at a rate > -0.04 MPa d^{-1} in all years of study. This rate of water stress development is similar to the rate under field (Fereres *et al.*, 1978; Turner *et al.*, 1986) or field-simulated (Jones and Turner, 1978) conditions, but slower than that measured in controlled-environment studies (Richardson and McCree, 1985; Sobrado, 1986; Toft *et al.*, 1987).

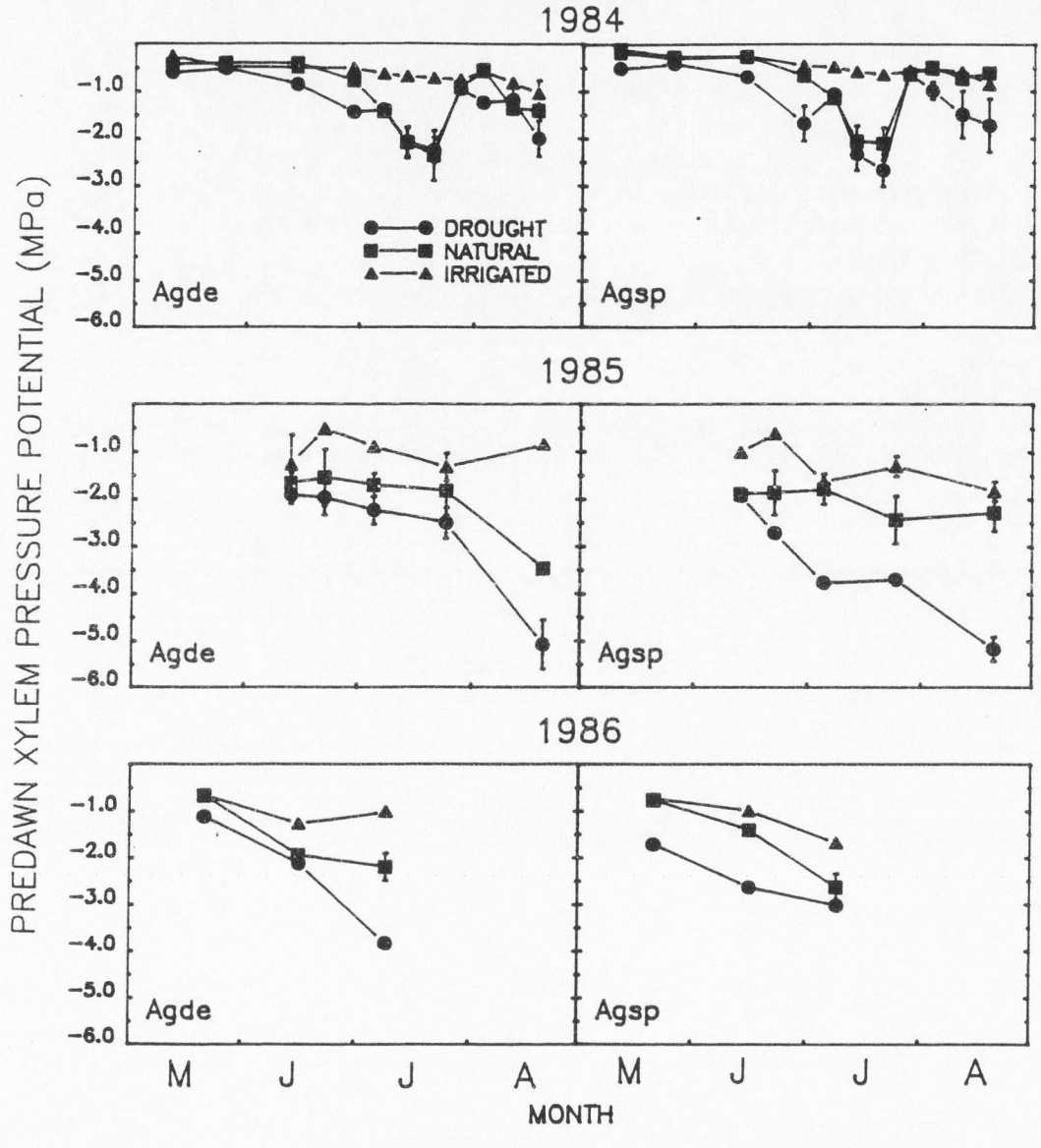


Fig. 2. Predawn leaf xylem pressure potentials during the experimental periods in 1984, 1985 or 1986 for unclipped A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural or irrigated conditions. Each point is the mean ± SE of 4 to 6 measurements. Error bars smaller than the symbols are omitted. Values for 1984 are unpublished data from D.A. Johnson.

Statistical Limitations

The experimental design had logistical limitations for the water and defoliation treatments. In the case of the rainout shelter, cost precluded treatment replication. As stated by Hurlbert (1984, p. 199)

> ...when the cost of replication is very great, experiments involving unreplicated treatments may also be the only or best option.

The defoliated plants could have been randomized and interspersed with control plants within the plots. However, this was not done for a number of reasons. During the 1984 growing season, the total aboveground (vegetative plus reproductive) production of sagebrush plants was more than 2 times greater when in competition with clipped than with unclipped bunchgrasses under all water levels. Thus clipping treatments affected the competitive background. It was necessary to include this component of the clipping response to maintain a realistic simulation of drought on rangelands. Also, each water level plot was not divided into more than 2 subplots because it would have meant working with a very small number of plants, since those on each subplot border could not have been used.

I will place emphasis on the results when differences in plant responses under the different treatments are large and statistical veracity of the data is obvious. Standard errors will represent a minimum measure of the plant to plant variability.

CHAPTER III

LEAF EXTENSION RATE OF TWO BUNCHGRASS SPECIES IN THE FIELD: INTERACTION OF WATER STRESS AND DEFOLIATION

Introduction

In semiarid and arid climates, grazing of pasture grasses often occurs under water stress (Ludlow, 1986). After grazing, high growth rates are necessary for plants to rapidly reestablish foliage. This is important if perennial grasses are to tolerate herbivory (Caldwell, 1984; Richards and Caldwell, 1985), especially when competing with undefoliated neighbors (Mueggler, 1972). One important component influencing growth rate of grasses is the rate of leaf extension, a process very sensitive to water stress (i.e., Boyer, 1970; Hsiao et al., 1970; Davies and Van Volkenburgh, 1983; Hsiao et al., 1985). Thus the recovery of plants from defoliation during drought could be limited by the negative effects of water stress on leaf extension rates.

Two tussock grasses were utilized in this research: Agropyron desertorum (Fisch. ex Link) Schult. and Agropyron spicatum (Pursh) Scribn. and Smith*. These species were selected because they are important components of the semiarid, sagebrush-bunchgrass ecosystem of the Intermountain West (Dewey and Asay, 1975; West, 1983). They also have a very similar phenology, physiology and

morphology (Caldwell et al., 1981; Nowak and Caldwell, 1984; Mueller and Richards, 1986) but differ in grazing tolerance (Caldwell et al., 1981). A. desertorum, introduced from Eurasia, is more tolerant of grazing than A. spicatum, a species native to the Intermountain West.

Leaf extension rates are often different in light and dark periods. Rates can be higher in the light than in the dark (Christ, 1978 a&b; Radin and Boyer, 1982; Thomas and Stoddart, 1984) or vice versa (Boyer, 1968; Bunce, 1977; Waldron et al., 1985). These differences in the timing of maximum leaf extension are probably the result of the combined effects of water status (Boyer, 1968; Waldron et al., 1985), temperature (Watts, 1972; Thomas and Stoddart, 1984) and light (Squire et al., 1983; Rawson and Munns, 1984; Borland and Farrar, 1985) on leaf growth. Elucidation of the dynamics of leaf extension in A. desertorum and A. spicatum is important to determine the sequence of leaf growth in these species. The relationship of these dynamics to leaf water status and air temperature under field conditions is also of concern. Determining these relationships could allow a basis for a mechanistic understanding of the effects of leaf water status and air temperature on leaf extension of these tussock grasses.

The present study aimed to quantify leaf extension rate of A. desertorum and A. spicatum under different water and clipping treatments and to relate this process to leaf water

status and air temperature under field conditions. The two major objectives were to determine:

1. the effects of water stress and water stress plus clipping during one or more years on the rate of leaf extension in A. desertorum and A. spicatum and,

2. the diurnal course (or pattern) of extension growth in A. desertorum and A. spicatum and the relation of this course to leaf water status and air temperature.

Materials and Methods

Measurements

Leaf extension was determined using a precision resistor and a pulley apparatus similar to that reported by Christ (1978a) and Takami et al. (1982). The distal end of a rapidly-expanding lamina was connected to a precision resistor by a polyester thread running over a pulley, counter-weighted so that the leaf was under a constant tension of approximately 10 g. Similar weights have been used in leaf growth rate studies on maize (Watts, 1974; Penning De Vries et al., 1979), wheat (Penning De Vries et al., 1979), bean (Davies and Van Volkenburgh, 1983), birch and sycamore (Taylor and Davies, 1985, 1986) and grape (Shackel et al., 1987). Any length change in the leaves registered an output change in the precision resistor. A calibration was developed for each resistor relating changes in length (mm) to changes in resistance (ohms). As there

were no significant differences among instruments (F test, $P<0.05$), the following equation was used for all resistors to obtain leaf extension (Δ mm) from changes in output between successive scans (Δ ohm):

$\Delta mm = (\Delta ohm + 15.6428)/148.6781 \quad (r^2>0.99, P<0.001)$

The resolution of the precision resistors was 0.1 mm. Outputs were monitored on a data acquisition unit (Hewlett Packard 3421A) and recorded by using a digital cassette drive (Hewlett Packard 82161A). The smallest detectable change in length by the data logger was 0.2 mm.

During the growing seasons of 1984, 1985 and 1986, simultaneous measurements of 10 to 14 tillers (1 tiller per plant) of one species in several treatments or of species in the same treatment were made every half hour during 12 to 48 hour periods. Measurements were made on the youngest visible expanding leaf (1 to 3 cm; about 30 % or less of full expansion) of each selected tiller during the observation period. Measurements were made after the first week of June in 1984, 1985 and 1986 to exclude most culm internode elongation (Olson and Richards, 1988a). In the one measurement prior to June, 1986 (24-25 May), some culm internode elongation could have been added to actual leaf extension. One to three controls, using a stone instead of a growing leaf, were also scanned so that any effects due to wind, temperature, humidity or the equipment itself could be determined. This provided a correction factor for the

outputs of 0.211 mm ± 0.068 ($\bar{x}$ ± s.d., n=2133).

In 1985 and 1986, leaf total water and osmotic potential of monitored leaves were measured at the end of the observation period, during predawn, midday or late evening hours. During any 12 to 48 hour measurement period, additional leaf total and osmotic potentials were determined at different times of the day on the youngest expanding leaf of other plants. Leaf water and osmotic potentials were measured using thermocouple psychrometer chambers maintained in a water bath at 25 C. Measurements were taken in the psychrometric mode by applying a 5 mA cooling current for 15 sec. Plateau voltages were read with a Wescor HR 33-T microvoltmeter (Wescor Inc. Logan, Utah, USA). Each psychrometer was calibrated against NaCl solutions prior to use. Leaf water potential was determined after a 3.5 to 4.0 hour equilibration period. The leaf tissue was then frozen in liquid nitrogen (77 K), allowed to thaw for 3.5 to 4.0 hours, and the osmotic potential measured. Turgor was calculated as the difference between the leaf water and osmotic potentials. Any matric effect was assumed to be negligible. Matric potentials are generally quite small for most plant tissues (Wiebe, 1966; Boyer, 1967).

Pressure-volume (P-V) relationships were developed to correct for dilution of symplastic solution by apoplastic water (Tyree, 1976; Jones and Turner, 1978; Meinzer *et al.*, 1986). To establish P-V curves (Tyree and Hammel, 1972),

upper fully-expanded leaves were cut from field-grown tillers under distilled water at the level of the ligule. Leaves were then left under water in covered beakers in the dark for a minimum of 4 hours. The P-V relations were determined for drought- or irrigated-exposed leaves of both species by using a pressure chamber. After rehydration, the balancing pressure of pre-weighed leaves (saturated weight) was measured. Leaves were then reweighed and allowed to lose water. This procedure was repeated until the balancing pressure was close to -6.5 MPa. At completion, the dry weight of the leaf was determined after drying at 70 C for 48 hours. The contribution of xylem sap osmotic pressure to xylem water potential was assumed to be negligible in the P-V curve determinations.

Data from each individual leaf were analyzed by using the P-V curve analysis program developed by Schulte in 1987 (pers. comm.). The exponential model followed in this computer program expresses turgor pressure as a function of relative water content such that zero turgor pressure can be obtained at the turgor loss point (Schulte and Hinckley, 1985, pp. 1594). Shulte's program involves non-linear least squares fits and provides estimates for the symplastic water fraction (SWF) and other water relations parameters. Outputs from this program yielded curves that fitted the data well ($r^2 > 0.98$). Similar to the results of Toft et al. (1987) in Eustachys paspaloides, SWF was not significantly different

between species or water levels in this study (as indicated by overlapping 0.95 confidence intervals). Values obtained under the different treatments were then pooled and an estimate of 0.85 ± 0.06 ($\bar{x}$ ± s.e., n=7) SWF was obtained. This value is similar to those reported by Toft et al. (1987) for an African perennial grass. Values of measured osmotic pressure (π_m) were then corrected (π_c) by using the estimated 15 % apoplastic water fraction as follows:

$$\pi_c = \pi_m x\ 1.15$$

Turgor pressure values were increased by about 0.3 MPa after osmotic potentials were corrected.

Treatment comparisons were made by using t tests that did not assume the population variances to be equal (Ryan et al., 1976, pp. 140-142).

Results

Leaf Growth under different Water and Clipping Regimes

Twenty-four hour integrations of the daily courses of leaf extension provided a better measure for comparison among treatments than hourly extension rates. When measurements only a few days apart were compared, daily leaf extension of both species was at least 70% lower under drought than under irrigated conditions in June and July of 1984 (Table 1) and in June of 1985 (Table 1) and 1986 (Table 2). In 1986, both species had lower leaf water potentials under drought (mean=-1.95 MPa) than under irrigated (mean=

Table 1. Daily (24 hr) rates of extension of the youngest visible expanding leaf of undefoliated tillers of A. desertorum (Agde) and A. spicatum (Agsp) under different water regimes in 1984 and 1985. Values are 24 hour integrations of the daily course of leaf extension rate. Each value is the mean ± SE of between 6 and 8 tillers (1 tiller/plant).

		LEAF EXTENSION (MM D^{-1})	
DATE	WATER LEVEL	Agde	Agsp
1984			
JUNE 27	IRRIGATED	1.7 ± 0.5	3.0 ± 0.5
28	DROUGHT	1.0 ± 0.2	1.0 ± 0.3
JULY 13	IRRIGATED	7.1 ± 1.4	7.6 ± 1.0
14	NATURAL	1.6 ± 0.7	2.2 ± 1.1
17	DROUGHT	0.9 ± 0.5	0.3 ± 0.1
1985			
JUNE 22	IRRIGATED	6.4 ± 2.2	8.9 ± 1.4
19	DROUGHT	0.8 ± 0.5	1.8 ± 0.5

Table 2. Daily (24 hr) rates of extension of the youngest visible expanding leaf of defoliated or undefoliated tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought or irrigated conditions in 1986. Plants had been exposed to the same clipping-water level treatment combination since 1984. Values are 24 hour integrations of the daily course of leaf extension rate. Each value is the mean ± SE of between 5 and 7 tillers (1 tiller/plant).

			LEAF EXTENSION ($MM\ D^{-1}$)	
DATE (1986)			Agde	Agsp
JUNE 9 & 10	DROUGHT	DEFOLIATED	2.1 ± 1.0	1.6 ± 0.7
11& 12		UNDEFOLIATED	4.4 ± 1.0	4.4 ± 2.5
25& 26	IRRIGATED	UNDEFOLIATED	12.8 ± 0.9	13.4 ± 1.5

-1.38 MPa) conditions. At the same time, however, turgor pressures were similar (mean=0.8 MPa) in the two water levels. This resulted from the different water potential-turgor pressure relationships of leaves in the irrigated and drought plots (Fig. 3). Leaf turgor pressures were at least 0.15 MPa higher in water-stressed than in irrigated plants of both species at any given leaf water potential when regression lines of the relationship between water potential and turgor pressure are compared (Fig. 3).

The late defoliation treatments in 1984 (29 June) and 1985 (13 June) precluded regrowth production on drought-treated plants of both species. The earlier defoliation treatment in 1986 (18 May), however, allowed a small amount of regrowth under these conditions. Clipped and drought-treated plants of both species had the lowest leaf extension rates among all of the treatments in 1986 (Table 2). At that time, leaf water potentials (mean=-1.95 MPa) and turgor pressures (mean=0.74 MPa) were similar on clipped and unclipped plants of both species exposed to drought.

The two species usually had similar rates of leaf extension under each treatment (drought, natural or irrigated) during June and mid-July in 1984 (Table 1), and during June in 1985 (Table 1) and 1986 (Table 2). Similar results were obtained under all clipping treatments in June of 1986 (Table 2). However, undefoliated tillers of A. desertorum maintained higher leaf extension rates than

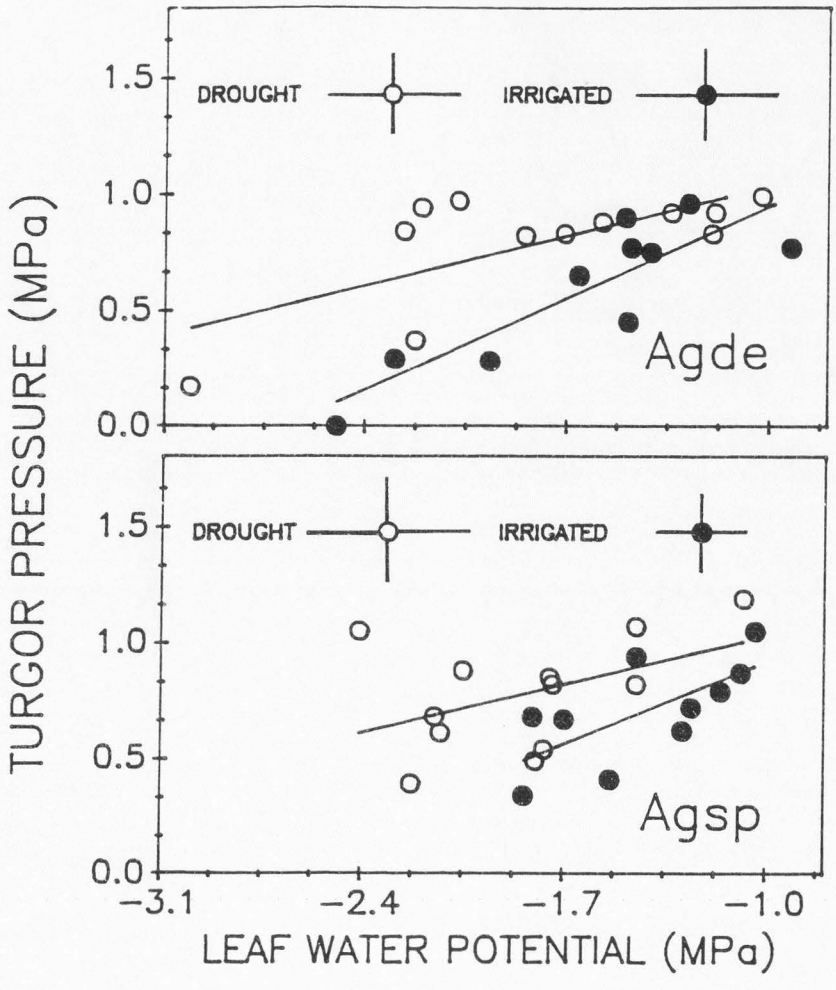


Fig. 3. Leaf turgor pressure versus leaf water potential for defoliated or undefoliated plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought or irrigated conditions in 1986. Plants had been successively exposed to the different clipping and water levels since 1984. Measurements were made at predawn, midday or evening hours. Each symbol is the mean of 6 observations. Horizontal and vertical bars on the labeled symbols represent ± an average SE of mean leaf water potentials and turgor pressures, respectively. Lines were generated by linear regression.

those of A. spicatum later into the growing season in 1984 under drought conditions (i.e., Table 1). At a similar time, predawn leaf water potentials were -2.3 MPa in A. desertorum and -2.7 MPa in A. spicatum (D.A. Johnson, unpublished data). At these leaf water potentials, and from the data obtained in 1985 and 1986 (Fig. 4), leaf extension rates were higher in A. desertorum than in A. spicatum. It also appears from Fig. 4 that greater leaf water potentials could be required in A. spicatum than in A. desertorum for sustained leaf extension.

Leaf Extension versus Water Status and Air Temperature

A typical example of the daily course of leaf extension is shown in Fig. 5. This pattern was consistent in all treatments and in the 30 observation periods in 1984, 1985 and 1986. The highest extension rates were obtained between 6 and 10 p.m. and the lowest rates between 2 and 8 a.m. The average rate of leaf extension for the light period was at least 1.2 times greater of that in darkness. Leaf extension during the night represented < 35 % of the total daily extension in both species.

A typical relationship for both species between the daily course of leaf extension rate and bulk leaf water potential is shown in Fig. 6 (D, E). This relationship was consistent for 9 observation periods in 1985 and 1986. The highest leaf extension rates were observed during early

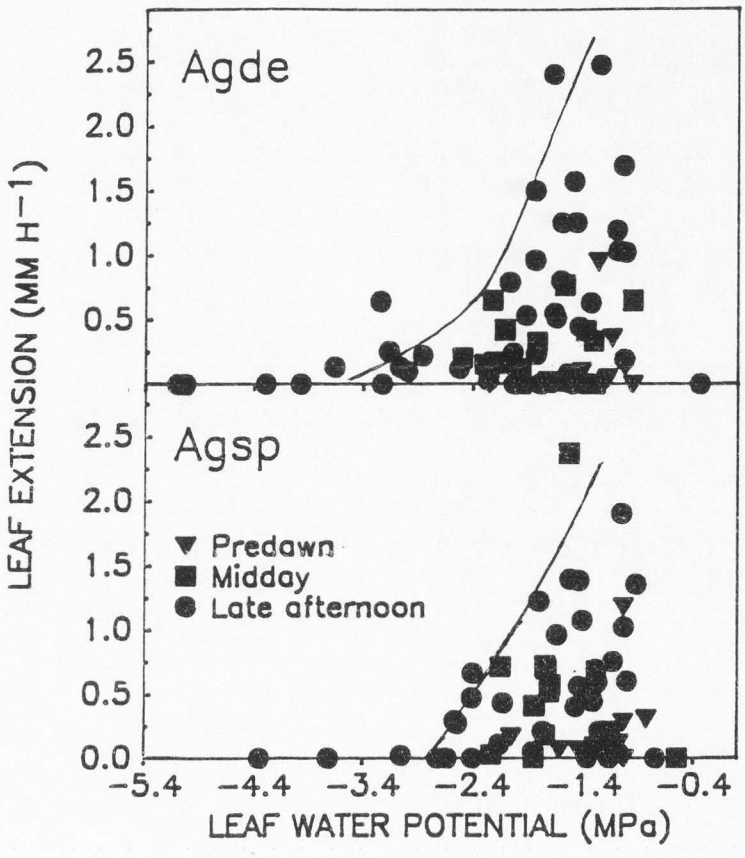


Fig. 4. Leaf extension rate at various leaf water potentials of field-grown defoliated or undefoliated plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought or irrigated conditions from 1984 until 1986. Data points represent averages of $4 \leq n \leq 7$ or are the leaf water potentials of the individual leaves being monitored for leaf extension at the end of each observation period. Measurements were made at predawn, midday or late afternoon hours in 1985 and 1986. A boundary line (Webb, 1972) has been visually-fitted on the body of data for each species.

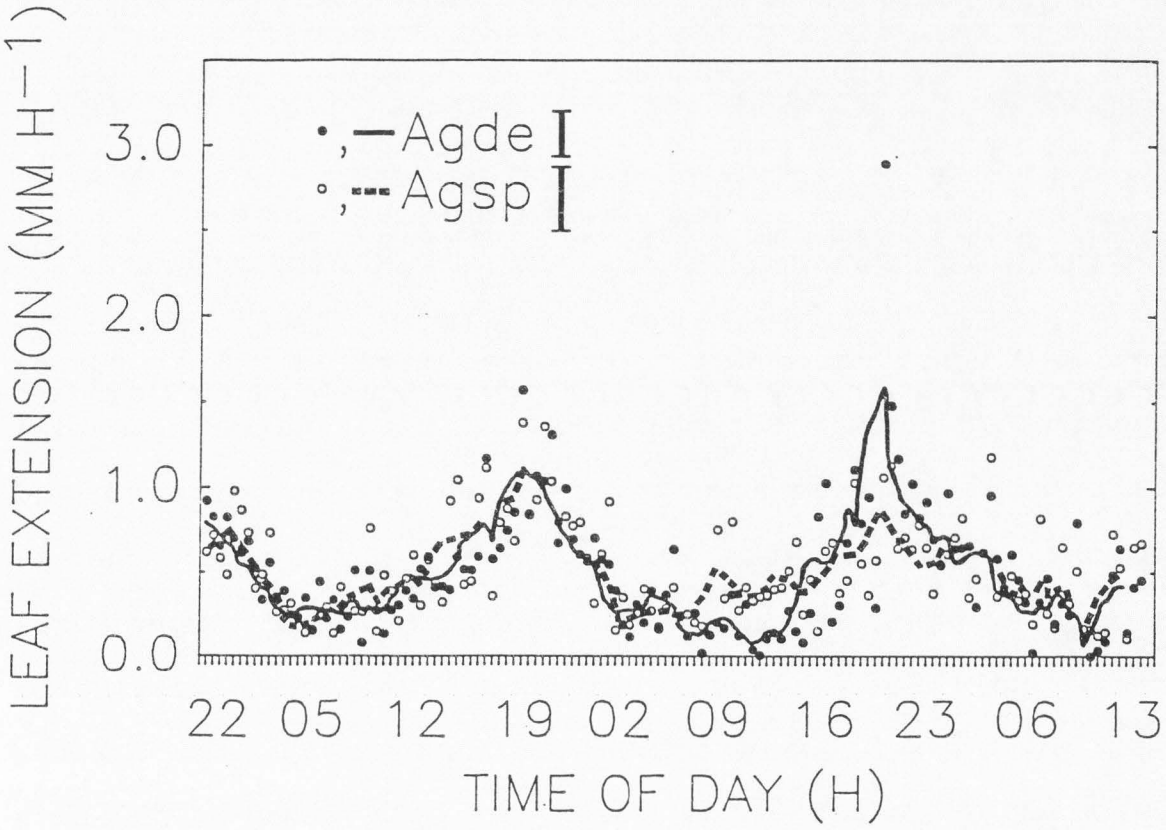
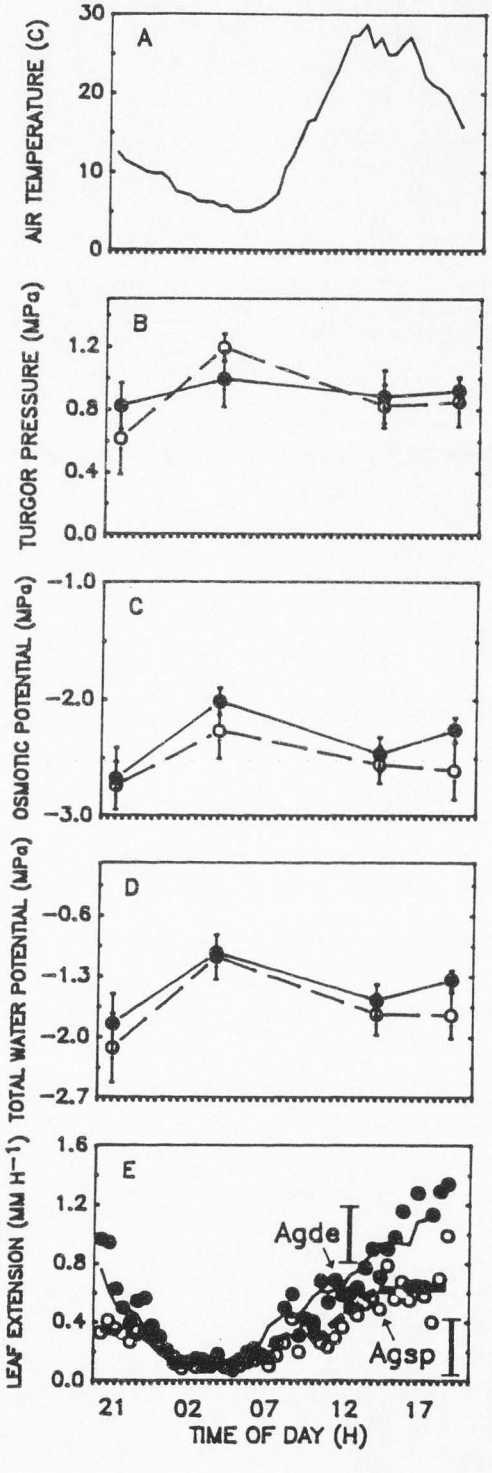


Fig. 5. Diurnal course of leaf extension rate for the youngest visible extending leaf on tillers of undefoliated and irrigated plants of A. desertorum (Agde) and A. spicatum (Agsp) during 25 to 28 June, 1986. Both species had been exposed to this clipping-water level treatment combination since 1984. Each symbol is the mean of 7 tillers (1 tiller/plant). The vertical bars indicate ± an average SE of the means for both species. A 2 hour running average of 4 half-hourly measurements is also shown as a solid or dashed line for A. desertorum and A. spicatum.

Fig. 6. Diurnal pattern of air temperature (A), leaf turgor pressure (B), osmotic potential (C), total water potential (D) and leaf extension rate (E) for undefoliated and drought-exposed plants of A. desertorum (Agde) and A. spicatum (Agsp) during 24 to 25 May, 1986. Air temperatures were scanned every 10 sec, and values were then integrated every 30 min. Turgor pressure and osmotic and total water potential values are the mean ± SE of 6 samples for both species. Symbols for Fig. 6 (E) are defined in Fig. 5.


A
AIR TEMPERATURE (C)
30
20
10
0
B
TURGOR PRESSURE (MPa)
1.2
0.8
0.4
0.0
C
OSMOTIC POTENTIAL (MPa)
−1.0
−2.0
−3.0
D
TOTAL WATER POTENTIAL (MPa)
−0.6
−1.3
−2.0
−2.7
E
LEAF EXTENSION (MM H⁻¹)
1.6
1.2
0.8
0.4
0.0
Agde
Agsp
21
02
07
12
17
TIME OF DAY (H)

evening hours in both species when leaf water potentials were between 0.4 and 1.0 MPa lower ($P < 0.08$) than at predawn on that day (see also Fig. 4). However, when a wider range of water potentials is considered, it is apparent from Fig. 4 that leaf extension is greater at higher than it is at lower leaf water potentials.

In 1986, the extension rate of leaves on drought- or irrigated-exposed tillers of A. desertorum and A. spicatum was not related to the turgor of the exposed leaf tissue (Fig. 6 (B, E)). While the rate of leaf extension varied throughout the day, turgor pressures were usually similar ($P>0.05$) at predawn, midday and early evening hours for both species. At times (i.e., A. spicatum in Fig. 6 (B)), turgor pressure was highest at predawn, when the rate of leaf extension was lowest. Maintenance of positive turgor pressure throughout the day was through adjustments in other water potential components. The diurnal trends of osmotic potential paralleled total water potential, thus allowing for turgor maintenance (Fig. 6 (B, C, D)).

The rate of extension closely followed variations in air temperature between evening and predawn hours (Fig. 6 (A, E)). Minimum growth rates for both species usually occurred at the time of minimum air temperatures (from 4 to 15 C in May, June or July of 1984, 1985 and 1986), which occurred during predawn or early morning hours. At times, however, > 5 C increases in the minimum air temperature

between consecutive nights did not result in greater leaf extension rates in either species.

At dawn, leaf extension rates showed a lag of approximately 2 to 4 h in relation to air temperature before they started increasing. After midday, when air temperatures decreased, leaf extension rates kept increasing toward their evening maximum, when air temperatures were between 15 and 22 C in June and July of 1984, 1985 and 1986 and turgor pressures were > 0.5 MPa in 1986. These patterns of diurnal variation of air temperature and rate of leaf extension resulted in a relationship between these two variables (e.g., Fig. 7), which was consistent in the 30 observation periods in the three years of study.

Discussion

This study looked at growth of the youngest visible extending leaf on tillers of A. desertorum and A. spicatum. At the same time this leaf was extending, however, older leaves were senescing in the same tiller. For example, youngest visible leaves of both species were extending under drought and natural conditions by mid July of 1984 (Table 1). At this time, however, leaf senescence was proceding at a greater rate than leaf production as indicated by the decline in the number of green leaves on tillers of both species (see Chapter IV).

It is well established that leaf growth decreases at

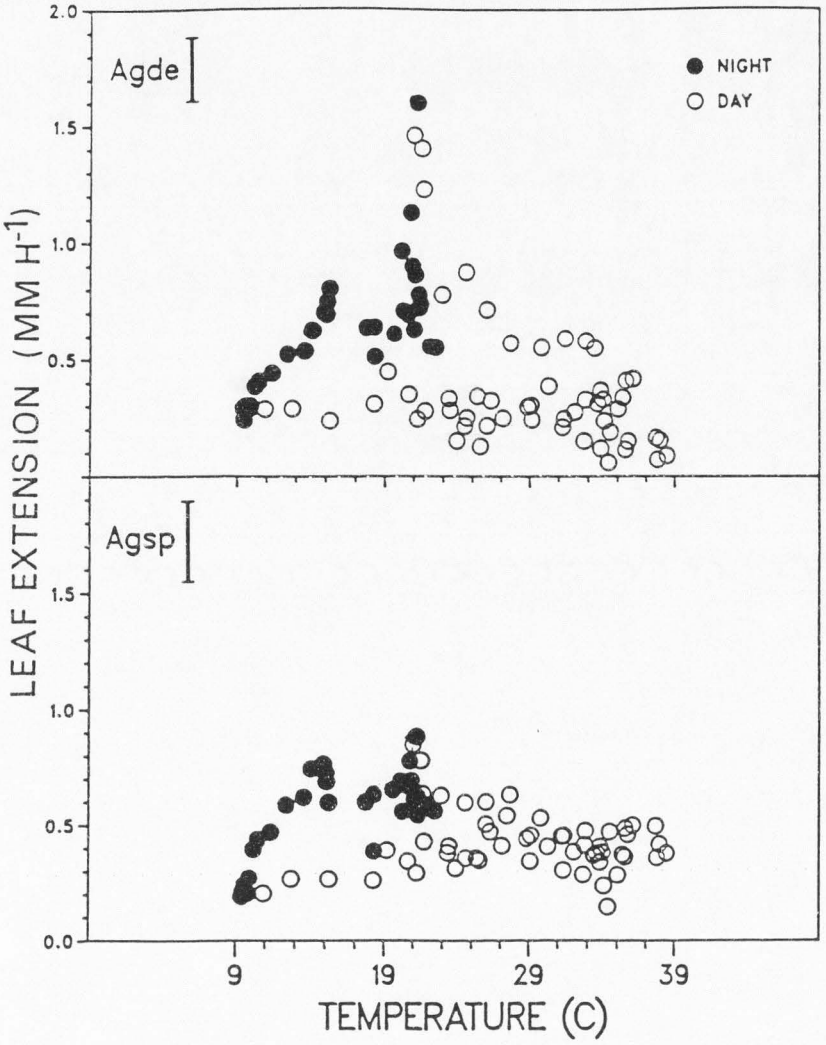


Fig. 7. Relationship between air temperature and leaf extension rate for undefoliated tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to irrigated conditions during 25 to 28 June, 1986. Both species had been exposed to this clipping-water level treatment combination since 1984. Air temperatures were scanned every 10 sec and values were then integrated every 30 min. Values of leaf extension rates are the mean of 7 tillers (1 tiller/plant). The vertical bars indicate ± an average SE of mean leaf extension rates for both species.

low leaf water potentials (Boyer, 1970; Hsiao et al., 1970; Squire et al., 1983; Westgate and Boyer, 1985; Toft et al., 1987). In agreement with this view, leaf growth rates in A. desertorum and A. spicatum were reduced by a long-term decline in leaf water potential (Fig. 4); water-stressed tillers of A. desertorum and A. spicatum had lower rates of leaf extension than those exposed to better moisture levels (Tables 1 and 2). In 1986, both species maintained similar turgor pressures under drought and irrigated conditions (see Fig. 3). The ability to maintain turgor when leaf water potentials decline under water stress has already been reported on other grasses (e.g., Jones and Turner, 1978; Sobrado, 1986; Toft et al., 1987). In some recent experiments, leaf growth of several species has also been inhibited in spite of maintenance of turgor pressure (Matthews et al., 1984; Van Volkenburgh et al., 1985b).

High carbohydrate availability in the extension zone of grass leaves appears necessary to support rapid growth (Davidson and Milthorpe, 1966; Schnyder and Nelson, 1987). Input of photoassimilates depends on green leaf area and photosynthetic rate per unit leaf area. Green leaf area in 1984 and 1986 were similar or lower under drought than under irrigated conditions for both species (Chapter IV). Also, it is well known that photosynthetic rates are reduced under water stress (Hsiao, 1973; Begg and Turner, 1976; Ludlow and Ng, 1976; Wilson et al., 1980) even with the occurrence of

osmotic adjustment (McCree, 1986). Consequently, the lower rates of leaf extension under drought may have been due in part to a shortage of assimilates for growth.

Drought conditions could have also decreased the extensibility of the cell walls on both species, thus increasing the minimum turgor required for growth. This has been proposed as a mechanism to explain reduced growth rates on water-stressed plants of several species (Davies and Van Volkenburgh, 1983; Matthews et al., 1984; Van Volkenburgh and Boyer, 1985; Sobrado, 1986). Decreases in cell wall extensibility can be produced by high levels of abscisic acid (Cleland, 1986; Kutschera and Schopfer, 1986). Abscisic acid can accumulate in young, growing leaves under water stress (Wright, 1977; Wright and Hiron, 1969; Walton, 1980). Increased cell wall extensibility and cell growth occur when the pH of the cell wall solution is lowered by hydrogen excretion from the cell interior (Van Volkenburgh and Boyer, 1985; Van Volkenburgh et al., 1985a). It seems possible that accumulation of abscisic acid in water-stressed plants inhibits excretion of hydrogen ions into the cell wall thus reducing wall extension and growth (Lawlor and Leach, 1985). Alternatively, decreased acidification may be an indirect result of decreased solute transport in tissue experiencing water deficit (Van Volkenburgh and Boyer, 1985).

It has been suggested that the rapid growth rates obtained after clipping on several grasses could be the

result of an improved leaf water status for the clipped plants (Hodgkinson, 1976; Christ, 1978b; Wolf and Parrish, 1982). In this study, clipping under drought did not enhance the water status of clipped tillers relative to unclipped controls. Similar results were reported by Nowak and Caldwell (1984) and Roundy et al. (1985) when these bunchgrasses were exposed to natural conditions. Despite having similar water status on the third year of repeated drought, clipped tillers of both Agropyron species had lower rates of leaf extension than unclipped ones (Table 2). At the same time, leaf area on clipped tillers was 10 % of that on unclipped controls (data not shown). Thus, photoassimilate availability could have been more limiting for leaf growth on clipped than on unclipped tillers of both species. This is similar to the conclusion reached by Davidson and Milthorpe (1966) for orchardgrass. Toft et al. (1987) also suggested that the initial depression of leaf extension in clipped plants of an African perennial grass was possibly due to a shortage of assimilates for growth.

Considerable scatter was observed in the relationship between leaf extension rate and leaf water potential. Similar results have been found for various crop and forage species (Ludlow and Ng, 1976; Penning De Vries et al., 1979; Squire et al., 1983; Toft et al., 1987). Some of this variation could be explained by differences in air temperature between evening and predawn hours or in solute

potential between plants exposed to drought and irrigated conditions (as suggested from Fig. 3, see also Squire et al., 1983). Other possible sources of variation in leaf extension rates are changes in resource availability between day and night (Gordon et al., 1982; Borland and Farrar, 1985), in the minimum turgor required for growth in response to water stress (Van Volkenburgh and Boyer, 1985; Sobrado, 1986), and in the extensibility of the cell walls between day and night hours (Taylor and Davies, 1986). Additionally, measurements of leaf water potential and turgor pressures in this study represent an average for all cells in the exposed lamina that was sampled. Grass leaves, however, grow from a basal meristem located inside the protective sheaths and leaf bases of older leaves (Barlow, 1986). Water potentials and turgor pressures have been shown to be different in the zone of extension at the base than at more distal, exposed positions in expanding leaves (Westgate and Boyer, 1984; Boyer et al., 1985). Thus the lack of a direct relationship between the water potential measurements (total and turgor) in A. desertorum and A. spicatum and the rate of leaf extension is not suprising.

The rate of leaf extension is a dynamic process controlled by a complex of physical and biological factors (Baker et al., 1985). Diurnal extension of both species was characterized under all water levels by higher daytime than nighttime rates with a maximum around sunset and a minimum

around sunrise (Figs. 5 and 6 (E)). Generally similar diurnal patterns of leaf extension have been observed in other grasses (Johnson, 1969; Watts, 1974; Christ, 1978a; Körner and Woodward, 1987). The diurnal course of leaf extension was opposite to the pattern of leaf water potential or leaf turgor, which were lower or similar during the day than at night (for example, Fig. 6 (B, D, E)). This discrepancy has been previously observed (Watts, 1974; Chu and Kerr, 1977; Cutler et al., 1977; Van Volkenburgh and Boyer, 1985; Van Volkenburgh and Cleland, 1986; Shackel et al., 1987) and may be due in part to the effects of low night temperatures. Low temperatures may decrease leaf growth at night by reducing the rate of synthesis of cell wall components, the delivery of cell wall loosening factors (e.g., hydrogen) and/or the transport of structural materials into the cell wall; these are metabolic factors of primary importance in the growth process (Cleland, 1981; Lawlor and Leach, 1985). Reduced leaf extension at night of various field-grown plants has also been attributed to low temperature effects (Williams and Biddiscombe, 1965; Johnson, 1969; Watts, 1974; Cutler et al., 1977).

Substantial temperature increases between successive nights, however, did not always cause increases in nighttime leaf extension in both Agropyron species. This suggests that factors, other than temperature, could also be controlling leaf extension at night. Another source of reduced growth

during night periods could be a shortage of carbon assimilates for cell wall synthesis; current assimilates could be used rapidly during the day and have a short-term storage such that they are insufficient to maintain high rates of leaf extension during darkness (Boyer, 1968; Christ, 1978b; Gordon et al., 1982; Takami et al., 1982; Rawson and Munns, 1984; Borland and Farrar, 1985). Leaf growth at night could also be restricted by decreased acidification and extensibility of the cell walls (Taylor and Davies, 1986).

In June and July, low temperatures at night could limit leaf growth in A. desertorum and A. spicatum. However, acclimation to cool temperatures in these cool season grasses allows them to grow in early spring. At this time, availability of water is not likely to limit regrowth in these species. The extensibility of the cell walls, rather than turgor pressure, could be a major factor in determining grass leaf extension at low temperatures (Woodward and Friend, 1988).

The response of leaf extension rate to the diurnal increase in temperature was often delayed by 2 to 4 hours. Similar lagged responses of leaf growth to temperature have been reported (Williams and Biddiscombe, 1965; Kanninen, 1985 and references therein) and attributed to either effects of lagged soil temperatures directly or changes in the water balance of the growing tissue. Highest rates of

leaf extension were around sunset for both species (Fig. 5 and 6 (E)). This may have been the result of adequate temperatures (15 to 22 C), turgor pressures (> 0.5 MPa) and carbohydrate availability for growth at this time. During a diurnal cycle, total nonstructural carbohydrate concentrations in leaves of several species have been found to be highest during evening hours (Mason and Maskell, 1928; Greenfield and Smith, 1973; White, 1973; Cutler et al., 1977).

This study demonstrated that water stress reduced leaf growth in A. desertorum and A. spicatum. By the third year of repeated treatments, leaf growth in A. desertorum and A. spicatum was lowest under the combination of drought and defoliation, which severely limited the amount of regrowth produced under these conditions (see Chapter IV). These results indicate that reduced leaf extension rates could limit the recovery of these species from defoliation during drought after plants had been successively grazed under drought for > 2 years. Leaf extension rates during the night, when maximum leaf water potentials and turgor pressures were observed, were less than those during the day. Even though air temperature was probably a major factor controlling leaf growth at night, other factors also appear to be involved. More controlled and detailed studies are needed to adequately explain the causes underlying the diurnal variation of leaf growth in A. desertorum and A.

spicatum as have been observed in this study.

CHAPTER IV

TILLER DEMOGRAPHY AND GROWTH OF TWO BUNCHGRASS SPECIES: THE SIMULTANEOUS INFLUENCE OF DROUGHT AND DEFOLIATION

Introduction

A high capacity for new tiller formation and rapid growth of these tillers after defoliation are necessary for perennial grasses to tolerate grazing and maintain their position in the community (Caldwell, 1984). Tiller formation and growth are, however, very sensitive to water deficit. For example, water stress may prevent bud outgrowth compared to unstressed plants (Klepper et al., 1982; Norris, 1982; Nus and Hodges, 1986). Leaf surface area is also reduced by water shortage (Rozijn and Van der Werf, 1986; Sobrado, 1986; Bittman and Simpson, 1987). This may be associated with decreased leaf production (Marc and Palmer, 1976; Norris, 1982, 1985; Chapman et al., 1983), increased rate of leaf death (Finch-Savage and Elston, 1976; Karamanos, 1978; Dwyer and Stewart, 1987), reduced plant height (Denmead and Shaw, 1960; Stout et al., 1978; Turner et al., 1986), smaller size of individual leaves (Acevedo et al., 1971; McCree and Davis, 1974; Bunce, 1977) and/or reduced tiller longevity (Caldwell et al., 1981). When defolation occurs under water stress conditions, as is commonly the case for rangeland grasses (Ludlow, 1986), plant recovery may be severely limited. However, quantitative data to support this

observation are lacking.

Recent studies of plant morphology have used a modular approach, i.e. considering plants as aggregations of repeated units of structure (White, 1979). This approach allows repeated non-destructive censuses and was used in this study to measure components of growth on individual tillers of two tussock grasses, namely Agropyron desertorum (Fisch. ex Link) Schult. and Agropyron spicatum (Pursh) Scribn. and Smith*. These species were selected for study because they differ greatly in tolerance of grazing (Hyder and Sneva, 1963; Caldwell et al., 1981) and constitute an important resource in the semiarid rangelands of the Intermountain West (Cook et al., 1958; Rogler and Lorenz, 1983; West, 1983). Much evidence has been put forward concerning the effects of soil moisture on growth and yield in various grass species (i.e., Norris, 1982, 1985; Bittman and Simpson, 1987). However, no information is available on growth characteristics of tillers of A. desertorum and A. spicatum when exposed to drought or to the simultaneous influence of drought and defoliation in the field. However, this knowledge is essential to assure persistence of productive stands under grazing.

The objectives of this research were to determine the effects of water stress alone and with defoliation during one or more years on

1. leaf area and dry matter production and their components including the number of green leaves, rate of leaf production, tiller height, green blade length and width, and green stem plus sheath length in (parent) tillers of A. desertorum and A. spicatum.

2. new (daughter) tiller production and growth in A. desertorum and A. spicatum immediately after spring defoliation; measurements for components of leaf area and dry matter production by daughter tillers were the same as those for parents.

Materials and Methods

Sampling Procedures

Plants of both species were randomly selected for tiller measurements (6 plants/treatment in 1984 and 1985, 4 plants/treatment in 1986 when fewer plants remained for sampling because of previous plant harvests). Ten tillers on each plant were marked with wire loops around their bases. On every sampling date, shoots that had emerged since the previous observation period were similarly tagged in order of appearance with colored rings. Observations of tagged parent shoots began on 17 June in 1984, 6 April in 1985 and 12 April in 1986 and were repeated every 10 to 30 days. In 1984, cohort A daughter tillers were first observed at the first observation after clipping, cohort B tillers emerged between the first and second observation after clipping,

etc. In 1985, the first cohort observed after clipping was B, the second one C, etc. In 1984 and 1985, observations continued until all tillers senesced in response to summer water deficits or were eaten by grasshoppers (the largest population was of Melanoplus femurrubrum (De Geer)). Measurements included: phenological state, number of green leaves, number of new leaves, total height, green blade length (total length of all blades), green stem plus sheath length and production of new tillers. In 1985 and 1986, leaf width was also measured.

Phenological stages were vegetative, boot, reproductive, senescent (proportion from 10 to 90 %) and dead (all tissue brown). A tiller was classed as vegetative if any green color was visible on its leaf blades. Tillers that had all their leaf blades dry or no leaf blades (i.e., some tillers after the clipping treatment or tillers which had all their leaf blades removed by grasshoppers) were classed according to their degree of senescence.

A leaf was considered as born when its tip had emerged at least 5 mm from the enveloping sheath. New leaves were marked with little dots of black paint to ensure their recognition at later recordings. Rate of leaf production was calculated by dividing the number of newly emerged leaves by the number of days between measurements. Linear measurements were made with a ruler to the nearest mm. Tiller height was measured from the soil surface to the tip of the longest

leaf. Green blade length was measured from the ligule to the most distal green portion of the lamina. Combined green stem and sheath length was measured from the green portion of the plant part closest to the ground to the point of origin of a new leaf; this measurement included the green portion of the inflorescence when it was present. Width was measured at the leaf blade center.

Green leaf length (and width) have been extensively used to estimate leaf area (i.e., Kemp, 1960; Van Arkel, 1978; Chanda et al., 1985). For this purpose, measurements of length and width, as described above, were made on additional harvested tillers. Leaf blade and combined stem plus sheath surface area were determined separately. Leaf blades and sheaths were unrolled before being mounted for area determination while exposed stem-segments were cut in half. For mounting, scotch tape was laid on the working surface with the adhesive side up. Blades and sheaths were placed on the tape and flattened out so that their entire surface was in contact with the tape. The tape bearing the plant parts was then affixed to a sheet of paper and replicas were cut out from the paper. The surface area of these paper images was measured using a Licor (Lincoln, NB) Model 3100 area meter.

In 1984, tiller blade area was calculated only from green blade length because leaf width was not measured; the regression was

LOG_{10}tiller blade area=0.179+0.0192 blade length (n=525, r^2=0.68, $\underline{P}$<0.001). In 1985 and 1986, prediction of tiller blade area was improved substantially by incorporating leaf width in the equation:

tiller blade area=0.342+0.67 blade length x leaf width (n=439, r^2=0.88, $\underline{P}$<0.001). In 1984, 1985 and 1986, combined tiller green stem plus sheath area was predicted from green stem + sheath length:

tiller stem + sheath area =0.29+0.194 stem + sheath length (n=525, r^2=0.75, $\underline{P}$<0.001). Total tiller green surface area was calculated as tiller blade area + tiller stem plus sheath area. Growth rates were calculated following Radford (1967) as:

$$\text{growth rate} = (X_{t+i} - X_t)/i$$

where X was leaf length (cm) or area (cm^2), t was starting time (d), and i was the time increment (d).

Grass standing crop was measured at clipping time and/or at the end of the experimental periods in 1984 and 1986 by clipping between 4 and 6 individual tussocks/treatment to a 5 to 7 cm stubble height. Regrowth will be used here to refer to the production of new tissue after defoliation. Herbage accumulation will be used to refer to the measured increase in herbage mass from early spring growth to summer senescence including clippings and regrowth.

Treatment comparisons for natural and irrigated plots

(2 replicates each) were made with split-plot ANOVA with water regimes as main plots (see Tables 3, 4 and 5 in Appendix for details). Sequential observations of the same group of tillers were subjected to an analysis of repeated measurements. Results for the drought treatment were obtained from 1 replicate; therefore, only means are reported for this water level. Survival differences among cohorts of daughter tillers were analyzed with Peto and Peto's Logrank Test (Pyke and Thompson, 1986).

Results

Parent Tillers

Phenology

As more than 50 % of the unclipped A. desertorum tillers were reproductive in the drought plot in 1984 (Appendix Fig. 25), and because these tillers started to dry out by early August, A. desertorum began to senesce earlier than A. spicatum. In 1985 and 1986, however, unclipped and drought-exposed tillers of A. spicatum senesced earlier than those of A. desertorum (Appendix Figs. 26 and 27). This was also the case for clipped tillers of both species in 1984 to 1986 under all water levels (data not shown). In all three years unclipped tillers of A. desertorum and A. spicatum showed similar phenologies under natural and irrigated conditions until the beginning of August (Appendix Figs. 25 to 27). At this time in 1984 and 1985 a large population of

grasshoppers on the plots showed preference for the leaf material of A. desertorum, causing a faster transition from vegetative to senescent stages in A. desertorum than in A. spicatum.

In 1984, 1985 and 1986 for A. spicatum, and in 1984 and 1985 for A. desertorum, later stages of senescence were reached earlier in the drought than in the natural or irrigated treatment (Appendix Figs. 25 to 27).

Number of Green Leaves and Rate of Leaf Production

The number of green leaves (Fig. 8) and the rates of leaf production (Fig. 9) were usually greater in A. desertorum than in A. spicatum. Undefoliated shoots of A. desertorum in 1984, 1985 and 1986 and of A. spicatum in 1986 had fewer leaves in the drought than in the irrigated treatment (Fig. 8). Also, blades of both species were on average shorter (>6 % in 1984 and >12 % in 1985 and 1986) and narrower (>4 % in 1985 and >11 % in 1986) in the drought treatment than under better moisture levels.

Rates of leaf production fell at the final stages of development, with those in the drought treatment suppressed to a greater extent than in the other treatments in 1984 and 1985 (Fig. 9). Similar suppression effects of water stress on the rate of leaf production were obtained in 1986. At this time, the lowest rates of leaf appearance were observed on drought-exposed and clipped tillers of both species.

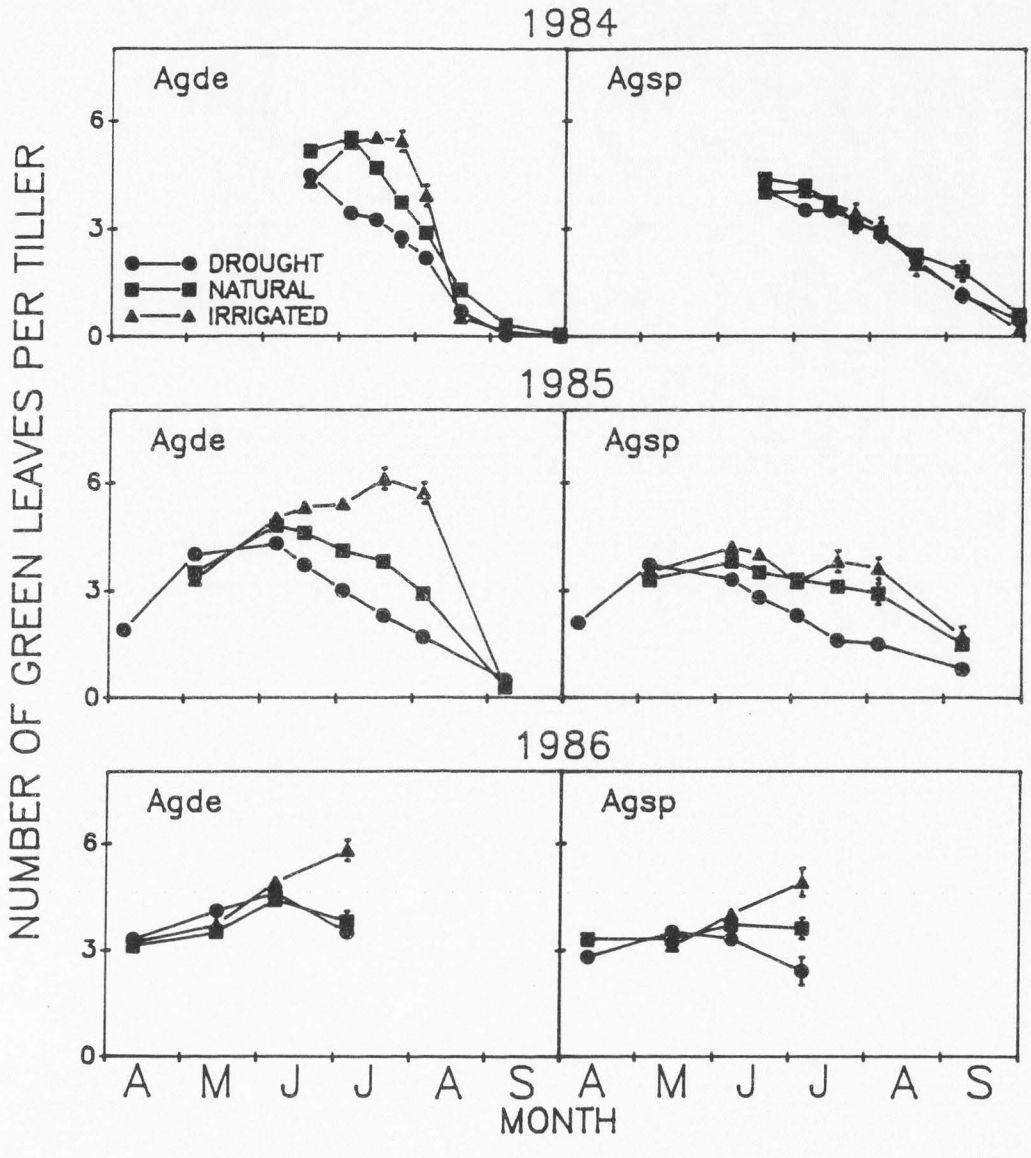


Fig. 8. Time course of the number of green leaves per tiller during the experimental periods in 1984, 1985 and 1986 on unclipped tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural or irrigated conditions. Each point is the mean ± SE of 60 determinations in 1984 and 1985 and of 40 in 1986. Error bars smaller than the symbols are omitted.

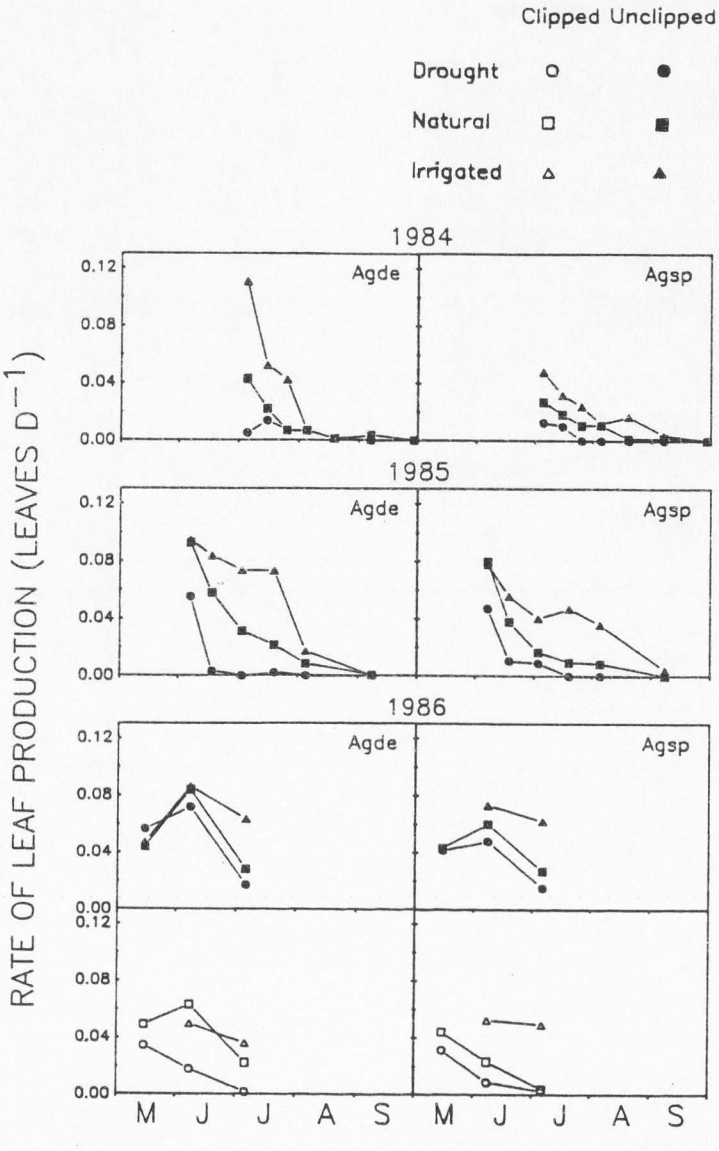


Fig. 9. The rates of leaf production during the experimental periods in 1984, 1985 and 1986 for unclipped or clipped tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural or irrigated conditions. Each point is the mean of 60 determinations in 1984 and 1985 and of 40 in 1986.

Tiller Height

Unclipped tillers of A. desertorum were 31 % taller than those of A. spicatum under irrigated conditions in 1986. Also, tillers of A. desertorum grew in height until later in the season than those of A. spicatum when watered in 1984 and 1985 or drought-exposed in 1986.

Tiller height was depressed by less available water in both species. For example, unclipped tillers of A. desertorum (in 1985 and 1986) and A. spicatum (in 1986) were >27 % smaller under drought than under irrigated conditions. Also, growth in height on clipped tillers of A. desertorum and A. spicatum was 5 to 7 cm in the natural and irrigated treatments but < 1 cm under drought conditions after the defoliation treatment in 1986.

Leaf Length and Area

Total length and area of blades on undefoliated shoots were greater (in 1984) or similar (in 1985 and 1986) in A. spicatum than in A. desertorum in the drought treatment. Blades of A. spicatum were on average > 1.25 times longer than those of A. desertorum under all water levels in 1984 and 1985 and under natural conditions in 1986. Length and area of combined stems and sheaths were greater (in 1984 and 1985) or similar (in 1986) in A. desertorum than in A. spicatum under drought conditions. Total leaf length (Fig. 10) or areas were similar in drought-exposed tillers of both species when values for blades and combined stems and

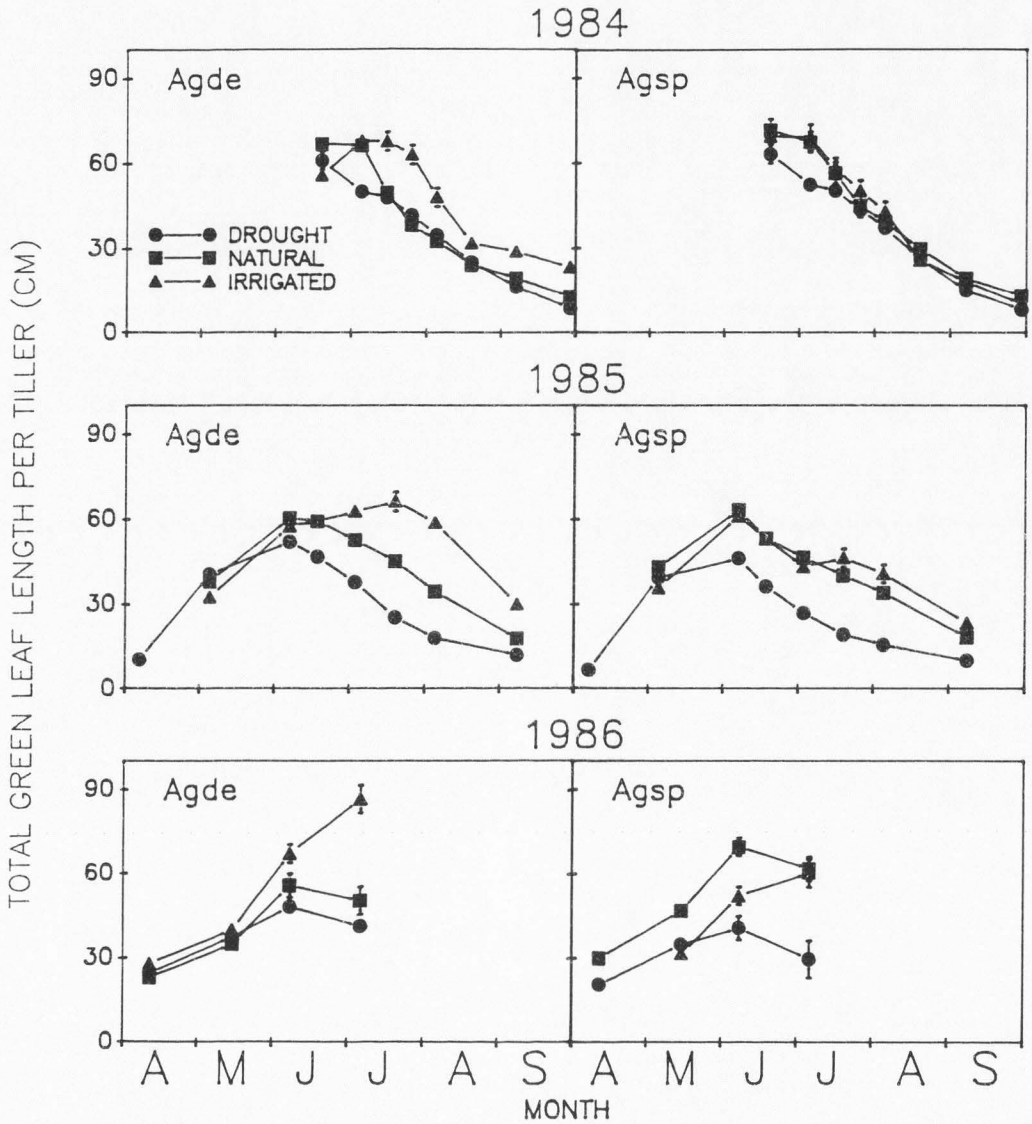


Fig. 10. Time course of the growth and decline in leaf length (total length for all blades plus stem and sheaths) during the experimental periods in 1984, 1985 and 1986 on unclipped tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural or irrigated conditions. Each point is the mean ± SE of 60 determinations in 1984 and 1985 and of 40 in 1986. Error bars smaller than the symbols are omitted.

sheaths were added in 1984 and 1985. In the third year of repeated drought (1986), however, maximum total area was 30% greater in A. desertorum than in A. spicatum. Total leaf length (Fig. 10) and area were also greater in irrigated tillers of A. desertorum than on those of A. spicatum in 1985 ($P<0.05$ for length) and 1986 ($P<0.01$ for length and area).

In the early spring that followed 2 years of repeated treatments (1986), unclipped tillers of A. desertorum and A. spicatum had >40 % total leaf length ($P<0.05$) or area than clipped ones under natural and irrigated conditions; these results were similar to those obtained under drought for both species.

Increased plant water deficit reduced growth in A. desertorum and A. spicatum. These species reached lower total leaf length in 1985 and 1986 under drought than under irrigated conditions (Fig. 10). Also, a highly significant correlation ($r=0.72$, $P<0.001$) was found between the maximum leaf area of both species and the mean leaf water potential in each treatment over the whole growth period in 1984, 1985 and 1986 (Fig. 11). Total leaf length (Fig. 10, $P<0.05$ in 1985 and 1986) and area ($P<0.01$ in 1986) also were less for natural than for irrigated and unclipped tillers in A. desertorum. Unclipped tillers of A. spicatum, however, had greater tiller blade area in 1985 ($P<0.05$) and blade, stem plus sheath and total length (Fig. 10) and area in 1986

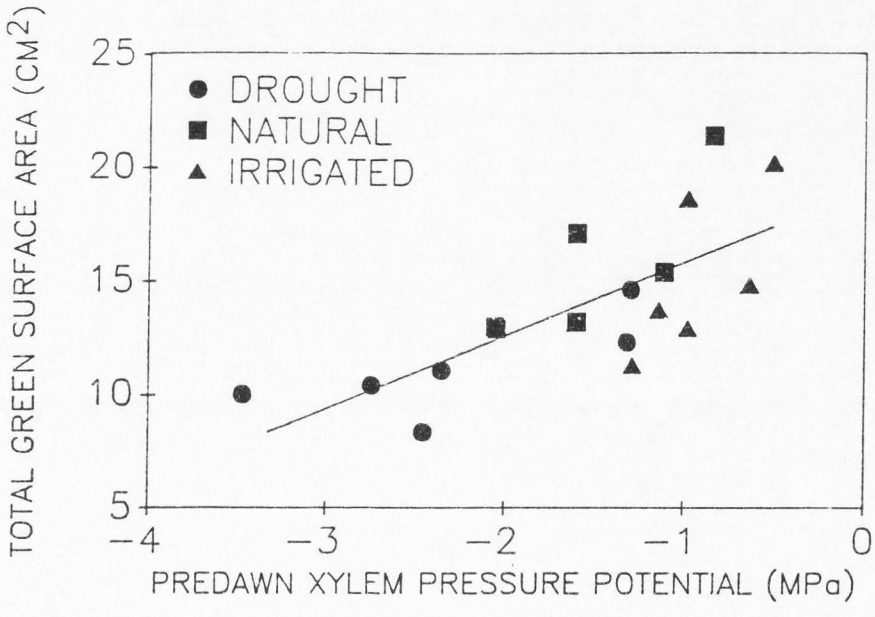


Fig. 11. Relation between the mean (40<n<60) maximum total (blade plus stem and sheaths) area on tillers of A. desertorum and A. spicatum and the mean predawn leaf xylem pressure potential under drought, natural or irrigated conditions during the experimental periods of 1984, 1985 and 1986. Values of leaf xylem pressure potential for 1984 are unpublished data from D.A. Johnson. A single linear regression was fitted ($Y=19.00 + 0.32X$, $r=0.72$, $P<0.001$) after separate regressions for both species and the three years of study were not statistically different.

($P<0.01$) under natural than under irrigated conditions.

Between May and early June in 1985, growth rates for total length or area on unclipped tillers of both species were 0.16 cm d^{-1} or -0.01 cm^2 d^{-1} for the drought, 0.66 cm d^{-1} or 0.08 cm^2 d^{-1} for the natural and 0.78 cm d^{-1} or 0.12 cm^2 d^{-1} for the irrigated treatment. The lowest rates for total length or area at this time were observed on clipped and drought-treated tillers of both species (mean=0.08 cm d^{-1} or -0.09 cm^2 d^{-1}). Similar patterns were obtained in 1986, although rates were > 1.3 times higher. Irrigation prolonged tiller growth in both species, although to a larger extent in A. desertorum. After the first week of June in 1984 to 1986, growth rates became negative under water stress for both species. At the same time, however, growth rates were positive under irrigation for A. desertorum in 1984 and 1985 and for both species in 1986.

Dry Weight

Regrowth was at least 1.5 times greater in A. desertorum than in A. spicatum after the third consecutive year of clipping under drought and natural conditions. Herbage accumulation was also greater (>100 %) on drought-exposed tillers of A. desertorum than on those of A. spicatum in 1986 (Fig. 12).

Unclipped tillers of A. desertorum and A. spicatum accumulated > 2.6 times dry herbage than clipped ones in all water level treatments in 1986 (Fig. 12).

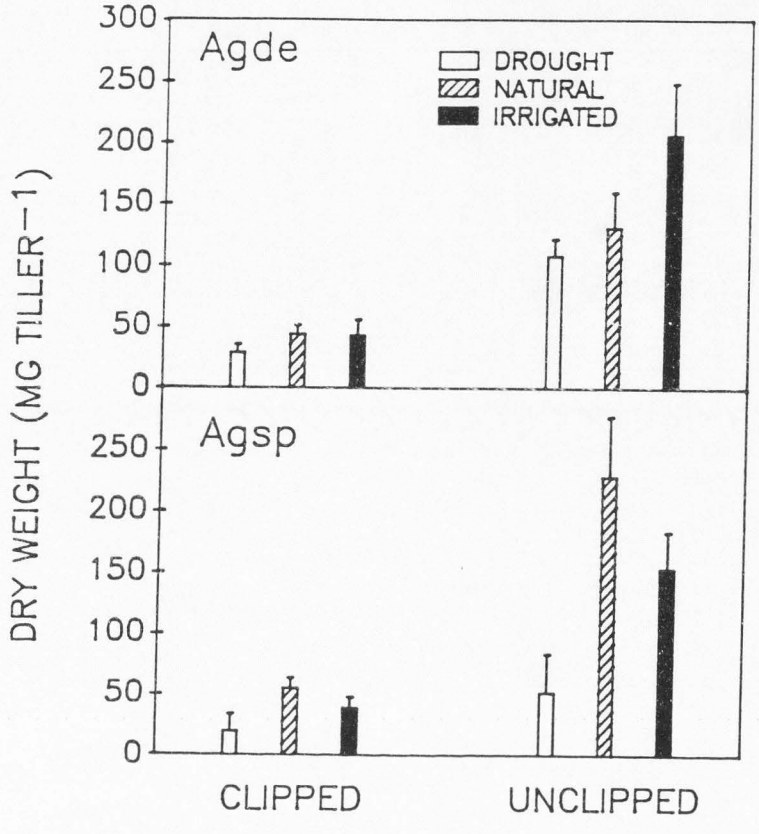


Fig. 12. Herbage accumulation on 31 July 1986 of unclipped and clipped tillers of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural or irrigated conditions. Plants of both species had been repeatedly exposed to these treatments since 1984. Each histogram is the mean of between 3 and 5 plants. Vertical bars represent 1 SE.

Herbage accumulation of A. desertorum and A. spicatum was similar or greater under drought than under natural or irrigated conditions in 1984 (data not shown). Following the third year of successive treatments (1986), however, herbage accumulation was > 1.2 times lower on drought- than on natural- or irrigated-exposed tillers of both species (Fig. 12). The lowest regrowth and herbage accumulation (Fig. 12) at this time (1986) were measured under the combination of drought and defoliation in both species.

Daughter Tillers

Total Production and General Characteristics

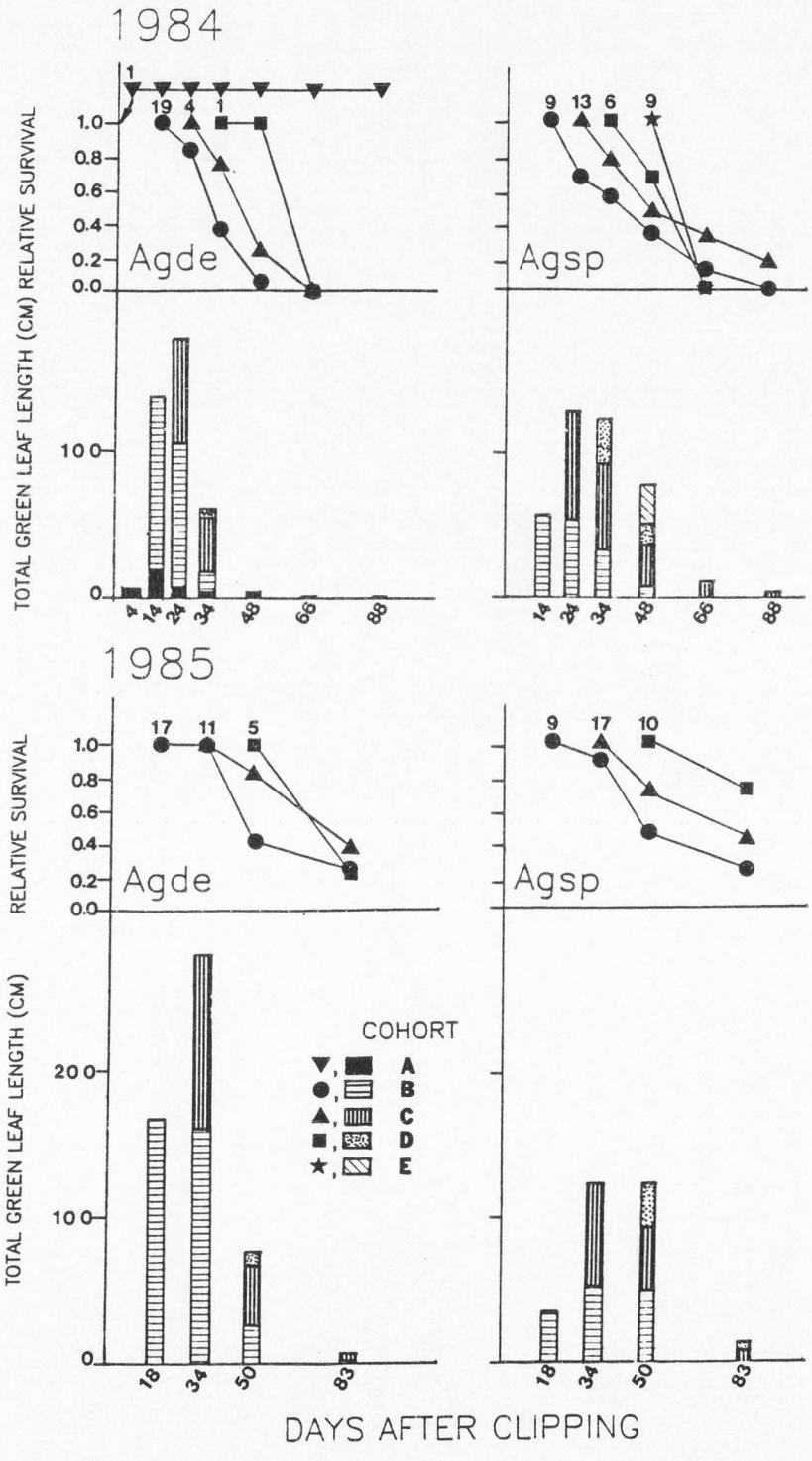
Control tillers of A. desertorum and A. spicatum in the drought treatment did not produce daughters in 1984 and 1985, and in 1986 only A. desertorum produced a few daughters (<0.03/parent). Clipped tillers of A. desertorum and A. spicatum did not produce daughters under drought in 1984 and 1985 and under natural conditions in 1985. Also, a few daughters (0.05/parent) were produced by clipped tillers of A. spicatum under natural conditions in 1984. This lack of daughter tiller production under drought and natural conditions in both years was the result of the timing of the defoliation treatments (after internode elongation; apical meristems were removed). Irrigation stimulated production of daughters by clipped tillers of A. desertorum (0.41 daughters/parent in 1984, 0.56 daughters/parent in 1985) and

A. spicatum (0.47 daughters/parent in 1984, 0.61 daughters/parent in 1985), even following the late clipping. The earlier defoliation treatment in 1986 (18 May) allowed some production of daughter tillers under drought in both species (<0.07 daughters/parent). At the same time, the largest daughter tiller production in clipped tillers of both species was observed under irrigated conditions (0.31 daughters/parent in A. desertorum, 0.25 daughters/parent in A. spicatum). Also, daughter tillers of A. desertorum in this year were taller and more vigorous under irrigated (means/individual: 15.1 cm for height, 30.9 cm for total leaf length) than under natural (means/individual: 4.5 cm for height, 7.7 cm for total leaf length) conditions.

Most (> 89%) of the daughter-producing parents of both species only elongated 1 or 2 axillary buds into tillers in 1984 to 1986 under all water levels; ocasionally, tillers of both species produced three or more daughters/parent under irrigated conditions.

Cohort Analysis

Two weeks after defoliation under irrigated conditions in 1984 and 1985, A. desertorum had produced twice the number of daughters than A. spicatum (cohort B in Fig. 13). These daughters had by then a similar green leaf length (mean=6.05 cm/daughter) in both species in 1984 but a greater green leaf length in A. desertorum (mean=9.8 cm/daughter) than in A. spicatum (mean=3.6 cm/daughter) in


1984
1985
Agde
Agsp
RELATIVE SURVIVAL
TOTAL GREEN LEAF LENGTH (CM)
COHORT
A
B
C
D
E
DAYS AFTER CLIPPING

1985. The total green leaf length of cohort B at this time was then twofold greater in A. desertorum than in A. spicatum in 1984, and 5 times greater in A. desertorum than in A. spicatum in 1985 (Fig. 13). In 1984, cohort B had a longer life-span for A. spicatum than for A. desertorum ($P<0.05$); however, in 1985 daughter tillers of cohort B had a similar survival in both species. In 1986, both species produced a similar number of daughters (mean=0.2/parent) of similar green leaf length (mean=8.7 cm/daughter). These daughters showed, however, a larger ($P<0.05$) proportional survival for A. desertorum (100 %) than for A. spicatum (62 %).

The number of survivors of any given cohort and its average green leaf length usually declined as the growing season progressed (Fig. 13). As a result, the relative contribution of that cohort to the total length accumulated over all cohorts also diminished. After mid-July in 1984 and 1985, clipped and unclipped tillers of A. spicatum produced more cohorts and/or a greater number of individuals/cohort than A. desertorum under natural or irrigated conditions (i.e., cohorts C to E in Fig. 13); this led to greater green leaf lengths in the grazing-sensitive than in the grazing-tolerant species late in the season.

Cohorts produced later (August, cohorts D and E) in the growing season on clipped plants of A. desertorum and A. spicatum had greater age-specific death rates than those

produced earlier (July, cohorts A to C) (i.e., irrigated A. desertorum in 1984 and 1985 and irrigated A. spicatum in 1984, Fig. 13, $P<0.05$). In 1984, these different-age cohorts had similar maximum values of green leaf length (mean=6.5 cm/daughter), number of green leaves (1.9/daughter) and tiller height (mean=4 cm/daughter) on both species. Similar results were obtained in 1985 for early versus late cohorts of A. spicatum under irrigation (means/daughter: 5.4 cm for leaf length, 1.9 for number of green leaves and 4.6 cm for tiller height). In this year, however, the maximum leaf length and tiller height were at least 2.5 times smaller on August-(mean=2.4 cm for length; 2.5 cm for height) than on July-produced cohorts of clipped and irrigated A. desertorum.

Clipped tillers of both species in 1984 produced a smaller number of cohorts with less than half as many tillers/cohort under natural than under irrigated conditions.

Discussion

During the studied growing seasons (1984 to 1986), tillers of adult plants of A. desertorum usually showed greater rates of blade production (Fig. 9) and delayed senescence (i.e., drought conditions, Appendix Figs. 26 and 27) than those of A. spicatum. Replacement of leaf blades has been shown previously to be greater in regrowth of A.

desertorum than in that of A. spicatum under natural conditions (Caldwell et al., 1981). Because the number of leaves present on a tiller results from the addition of leaves (births) and their deaths, the number of green blades was usually greater in A. desertorum than in A. spicatum under all water levels (Fig. 8). However, leaf blades of A. spicatum were on average 25 % longer than those of A. desertorum under drought and natural conditions. This resulted in similar or greater total blade lengths in the grazing-sensitive than in the grazing-tolerant species under these water levels. On the other hand, green stem plus sheath length and area were usually greater in A. desertorum than in A. spicatum under all moisture regimes, but especially in the irrigated treatment where tillers of A. desertorum were taller than those of A. spicatum. Stem and sheath tissue is photosynthetically active in both species and can be an important source of photosynthate for regrowth (Caldwell et al., 1981; Richards and Caldwell, 1985).

Drought resistance was apparently greater in the grazing-tolerant A. desertorum than in the grazing-sensitive, A. spicatum, after they had been exposed to water stress or to the combination of water stress and defoliation during 3 consecutive years. The total green surface area of a tiller depends on the number of leaf blades, length and width of these blades and length and width of stem plus sheaths. These parameters combined to give similar total

green surface area/tiller in A. desertorum and A. spicatum under drought conditions in 1984 and 1985. In 1986, however, total green surface area and dry matter yields (Fig. 12) were greater on drought-exposed tillers of A. desertorum than on those of A. spicatum. At the same time, the percentage reduction in shoot dry weight in the drought plot as compared to shoot dry weight in the natural or irrigated plot was greater for A. spicatum than for A. desertorum (Fig. 12). A. desertorum is known for its resistance to water stress (Pepper et al., 1953; Hull and Klomp, 1966).

Irrigation promoted growth in A. desertorum (i.e., Figs. 8, 10 and 12; Cook et al., 1958) but not in A. spicatum. A. spicatum showed a lower tiller height, total leaf length (Fig. 10) and area (not shown), and dry matter yield (Fig. 12) under irrigated than under natural conditions in 1986; thus water may have been in excess in the irrigated plot for the grazing-sensitive bunchgrass although the precise cause for this growth reduction is not known. Yield reductions because of poor aeration have been reported in other grasses (i.e., Etherington and Rutter, 1964).

In the early spring that followed 2 consecutive years of treatments, tiller number (Chapter V), length, area and yield (Fig. 12) were lower on late-clipped (after internode elongation) than on unclipped tussocks of A. desertorum and A. spicatum under all water levels. These results are

consistent with those of Heady (1950) and Wilson et al. (1966) for A. spicatum, Olson and Richards (1988b) for A. desertorum and Neiland and Curtis (1956), Stout et al.(1980, 1981) and Hall et al. (1987) for other forage grasses. Clipping or grazing during or after internode elongation (Heady, 1950; Wilson et al., 1966; Olson and Richards , 1988b) thus was apparently especially damaging to the persistence of A. desertorum and A. spicatum in the stand. On the contrary, early grazing (before internode elongation) of A. desertorum seldom affected tiller replacement in this species (Olson and Richards, 1988b).

Water stress reduced the total green leaf area on tillers of A. desertorum and A. spicatum (Fig. 11), as it does in many other grasses (i.e., McCree and Davis, 1974; Rozijn and Van der Werf, 1986; Bittman and Simpson, 1987). Reduced photosynthetic area was associated with smaller tillers that had fewer leaves (Fig. 8) of a smaller size under drought. Both species also had reduced exposed leaf area under water stress due to leaf rolling (pers. obs.). Withholding water reduces plant height (Denmead and Shaw, 1960; Stout et al., 1978; Turner et al., 1986), leaf number and size (Marc and Palmer, 1976; Karamanos, 1978; Norris, 1982) in several other plant species.

Reductions in growth by long-term drought stress in this study were due to lower growth rates and shorter growth periods under these conditions. For example, the rate of

leaf production for both species was lower and ceased earlier in the driest than in the wettest treatment (Fig. 9). Similar results have been reported for Lolium, Dactylis and Festuca species by Norris (1982, 1985), in Lolium perenne, Agrostis spp. and Trifolium repens by Chapman et al. (1983), and in oleaginous species by Marc and Palmer (1976) and Karamanos (1978). Also, during May in 1985 and 1986 (a time of major shoot growth in A. desertorum and A. spicatum (Caldwell et al., 1981)), rates of leaf length or area increase were more than 3 times lower under drought than under better moisture levels. Water stress is one of the most well-known causes of reduction in growth rates (i.e., Hsiao, 1973; McCree and Davis, 1974; Hoogenboom et al., 1987). Because the components of leaf area production were all reduced by water deficits, herbage accumulation was also lower under drought than under natural or irrigated conditions (Fig. 12). This is similar to results obtained with these (Cook et al., 1958) and other grasses (Etherington and Rutter, 1964; Norris, 1982, 1985; Bittman and Simpson, 1987).

Consequently, growth was reduced by repeated late-defoliations or drought stress in both species. However, in 1986 (which reflects the cumulative effects of treatments in the 3 preceding years), the reduction of growth was even greater under the combination of drought and defoliation. The rates of leaf (Fig. 9), daughter tiller, total length

and leaf area production, and height growth all were lowest under drought and defoliation conditions. In addition, the total (Fig. 12) and regrowth yields of A. desertorum and A. spicatum were the lowest under the combined influence of drought and clipping in 1986. Similar results were obtained by Mohammad et al. (1982) for A. desertorum, after greenhouse-grown plants had been severely defoliated (80 % foliage removal) under water stress (leaf water potential= -1.5 MPa) for only 1 year. When A. desertorum and A. spicatum were defoliated (85 to 90 % herbage removal) for the first time (29 June 1984) under a similar leaf water stress (-1.5 MPa at predawn, see Fig. 2), however, dry matter yield was similar or greater for drought- than for natural- or irrigated-exposed plants of these species. This difference between our field and Mohammad et al. (1982)'s glasshouse study cautions against extrapolating results obtained in environmentally-controlled investigations to field conditions.

Mohammad et al. (1982) also found that A. desertorum was most productive when clipping removed about 40 % of the foliage under water stress (leaf water potential= -1.5 MPa). They suggested that production and survival of A. desertorum should be enhanced by light or moderate grazing under drought because of a decrease in the amount of transpiring surface area. Leaf blade water status in A. desertorum and A. spicatum did not improve in this field study, however,

after the plants were severely clipped under water stress (Chapter III).

Grasshoppers are important insect herbivores of A. desertorum (J. Hansen, pers. comm.) and A. spicatum (Rogers and Uresk, 1974). It has been also shown that they select their food (Mulkern, 1967; Rogers and Uresk, 1974). After mid-July in 1984 and 1985, there was a severe grasshopper infestation on our plots. The largest population of grasshoppers was of Melanoplus femurrubrum, but M. sanguinipes, M. bivittatus, M. packardii, Phoetaliotes nebrascensis and 6 other species of the subfamily Oedipodinae were also present. These, or some of these, grasshopper species clearly preferred leaf blades of A. desertorum over those of A. spicatum (pers. obs.). This observation is corroborated by the sharp decline of the number of green leaves on parent tillers of A. desertorum at this time (see Fig. 8). The greater number of daughter tiller cohorts with more individuals/cohort in A. spicatum than in A. desertorum after mid-July (i.e., Fig. 13) could be the result of a greater predation by grasshoppers on A. desertorum daughter tillers. Some daughter tiller production in A. desertorum could have been undetected because observations were made every 10 to 30 days. Perhaps this was the result of a greater selection by grasshoppers against older leaf material (i.e., that of earlier-produced cohorts).

Grasshoppers may also have been important in increasing the death risk of cohorts produced late (August) compared to earlier (July) produced cohorts on clipped and irrigated tillers of A. desertorum and A. spicatum. Alternatively, the greater age-specific death rates in later- than in earlier-produced cohorts of A. desertorum in 1985 may be related to the smaller size of those individuals born in August. Solbrig et al. (1980, 1988) reported that seedling mortality was higher at any time among the smallest individuals for several Viola species. Similar results were found by Fowler and Antonovics (1981) for Plantago lanceolata.

This study demonstrated that a mild water stress or clipping under these conditions during one growing season (i.e., 1984) did not limit vegetative growth and potential yield in A. desertorum and A. spicatum. However, vegetative growth and/or productivity were severely reduced when predawn leaf water potentials of these species fell below -2.5 MPa during 2 or more growth periods. The greatest limitation to regrowth on tillers of both species was observed under the simultaneous influence of drought and defoliation for more than 2 years. Repeated late grazing of these species under long-term droughts (2 or more years) could then be expected to rapidly reduce the persistence of these forages in the community and open the way for invasion of less desirable species. Breman and Cissé (1977) reported that the species composition of Sahelian pastures was

changed and their carrying capacity reduced after they were exposed to drought or to the combination of drought and grazing for 5 years. Future work that directs efforts toward determining the effects of earlier and/or less severe defoliations (than those used in this study) under drought in A. desertorum and A. spicatum would appear promising.

CHAPTER V

EFFECTS OF DROUGHT AND HERBIVORY ON BUD VIABILITY IN TWO CAESPITOSE GRASSES

Introduction

Perennial grasses of semiarid and arid rangelands may be repeatedly defoliated under water deficit conditions (Ludlow, 1986). When active meristematic tissues are removed by grazing, the reestablishment of a photosynthetic canopy depends on the production of new tillers through the activation of axillary buds (Hyder, 1972; Jewiss, 1972). Bud growth on annual and perennial grass species is controlled by endogenous growth regulators, abiotic factors and resulting interactions (Mitchell, 1953; Jewiss, 1972; Fletcher and Dale, 1974). The combined pressures of water and defoliation stress might interfere with axillary bud production, viability, and/or activation which may limit the regrowth potential of a particular species. Such a limitation might reduce stand longevity and contribute to the deterioration of rangeland vegetation. However, few quantitative data are available on the effects of the interaction between water stress and defoliation on tiller bud number and respiratory activity in perennial grasses.

The two important semiarid tussock grasses that were utilized, Agropyron desertorum (Fisch. ex Link) Schult. and Agropyron spicatum [(Pursh) Scribn. and Smith]*, differ greatly in grazing tolerance. These two species are

widespread in temperate semi-deserts of the northern hemisphere (West, 1983) and are very similar in physiological, morphological and phenological characteristics (Caldwell et al., 1981, 1983), including their responses to water stress and limits of tolerance. The difference in grazing tolerance of these two species under field conditions has been related to the greater ability of A. desertorum to produce axillary tillers and preferentially allocate carbon resources to regrowing shoot sinks (Caldwell et al., 1981; Richards, 1984; Richards and Caldwell, 1985).

The difference in grazing tolerance between the species could be altered by the combined effects of defoliation and water stress on axillary bud activity. This study sought to determine if the total number of metabolically active buds (potential axillary tillers) are reduced by concommitant drought and defoliation stress during two or more growing seasons. A second objective was to determine the relationship between the number of metabolically active buds and early spring growth of A. desertorum and A. spicatum that had been defoliated under drought in preceding years.

Materials and Methods

Tiller Bud Observations

Tillers of both species were sampled to determine effects of the previous year's drought and defoliation on

respiratory activity, size, and number of axillary buds. Between 3 and 12 intact tillers from 2 to 4 plants per treatment were harvested. One year old tillers were sampled in the early spring of 1986 (3 to 12 April) and 1987 (11 May). Growing tillers were harvested after defoliation in 1985 (27 to 30 June) and 1986 (21 May to 3 June).

Tiller and rhizome bud growth in grass species have been evaluated by tests in soil, agar and other water-saturated media (Johnson and Buchholtz, 1961; Spiers and Holt, 1970; Turner and Loader, 1980; Stoltenberg and Wyse, 1986). The triphenyl tetrazolium chloride (TTC) assay has also been used to evaluate metabolic activity (Dekker and Chandler, 1985). These techniques, however, are unable to distinguish between dead, and viable but totally dormant buds, which may still have the potential for future growth given appropriate conditions. Thus bud metabolic activity was evaluated visually, with TTC and with a vital stain, Evan's blue, in an attempt to minimize this limitation.

After dissection, bud length was measured from the prophyll tip to the lowest attachment on the tiller with an ocular micrometer. Bud location was mapped and identified following the terminology of Mueller and Richards (1986). The stem base was cut longitudinally with a razor blade leaving entire tiller buds on each side of the cut. Both halves were incubated in a TTC-phosphate buffer solution with 0.05 % (v/v) Dupont WK wetting agent at 30 C for 15 h

(Steponkus and Lanphear, 1967). TTC staining indicates enzymatic reduction of the tetrazolium salt to insoluble, red formazan by living tissues (Smith, 1951). A bud was considered metabolically active when the apex stained pink or red.

In 1987, buds that remained unstained after incubation with the TTC solution but were not visibly necrotic, were tested using the vital stain Evan's blue (0.25 % w/v). Evan's blue does not penetrate intact semi-permeable membranes (Gaff and Okong'O-Ogola, 1971). Longitudinal sections of TTC-unstained buds were soaked in Evan's blue for 15 to 20 minutes at room temperature (20 C). Excess dye was rinsed from the sections, which were then mounted in water and examined under a microscope. Buds killed by boiling water stained dark blue with the nucleii staining darker than the protoplast. Buds with a similar appearance were considered dead.

Early Spring Growth Measurements

Early spring growth was determined in 1986 and 1987 after 2 or 3 years of drought and defoliation treatments to evaluate cumulative effects and to compare to the bud activity data. Green leaf blade length and width, and stem and sheath length were measured with a ruler between 10 and 15 April 1986 before water stress developed and before defoliation that year. These measurements were taken on 10

tillers on each of 3 to 4 defoliated and undefoliated plants of both species. Regression equations were developed to calculate leaf blade area and total stem and sheath area from these linear measurements (see Chapter IV). Total surface area per tiller was calculated as leaf blade area plus total stem and sheath area.

Between 4 and 6 May 1987, 6 tillers per plant from 3 to 8 plants per treatment were harvested for leaf area determinations. Paper images of one-side leaf blade area and total stem and sheath area were measured with a Licor (Lincoln, NB) Model 3100 area meter. Green stems and sheaths were included in the leaf area measurements because they contribute substantially to total plant photosynthesis (Caldwell et al., 1981). The number of green tillers was counted on each of 3 plants per treatment on 12 May 1985, on 6 plants per treatment between 28 March and 6 April in 1986, and on 3 to 8 plants per treatment between 30 April and 2 May in 1987. Different numbers of plants were used because of limited availability of moderate-sized, healthy tussocks in each treatment plot. Total canopy green leaf area was calculated by multiplying the mean number of tillers present by their mean surface area.

Statistical differences among treatments were assessed using the Mann-Whitney U-Test (Zar, 1984).

Results

Early spring observations of tiller buds produced the previous year revealed three categories of bud viability. Some buds were highly decomposed and obviously dead. Other buds were apparently healthy, but did not exhibit respiratory activity as indicated by TTC, i.e. they remained unstained. The Evan's blue staining done in 1987 indicated that buds in this category were most likely viable (minimal or no stain uptake) but had inadequate respiratory activity to stain with TTC. These buds were probably dormant, not dead. A third group of buds showed a healthy appearance and highly active meristematic respiration as indicated by their red or pink staining in the TTC solution. Axillary buds on growing tillers were always in the second or third category.

Bud Characteristics immediately after Spring Defoliation

Axillary buds of both species in all treatments were sampled immediately after mid-spring defoliation in 1985 and 1986 to determine potential bud pools for regrowth. The water regimes had been in effect since October 1983 and defoliated plants had been clipped since 1984. By 1986, the average number of axillary buds per tiller was lowest ($P < 0.05$) in the drought treatment and clipped and unclipped tillers of both species had an average of between 2.5 and 3.5 axillary buds (Fig. 14). Bud numbers on clipped and

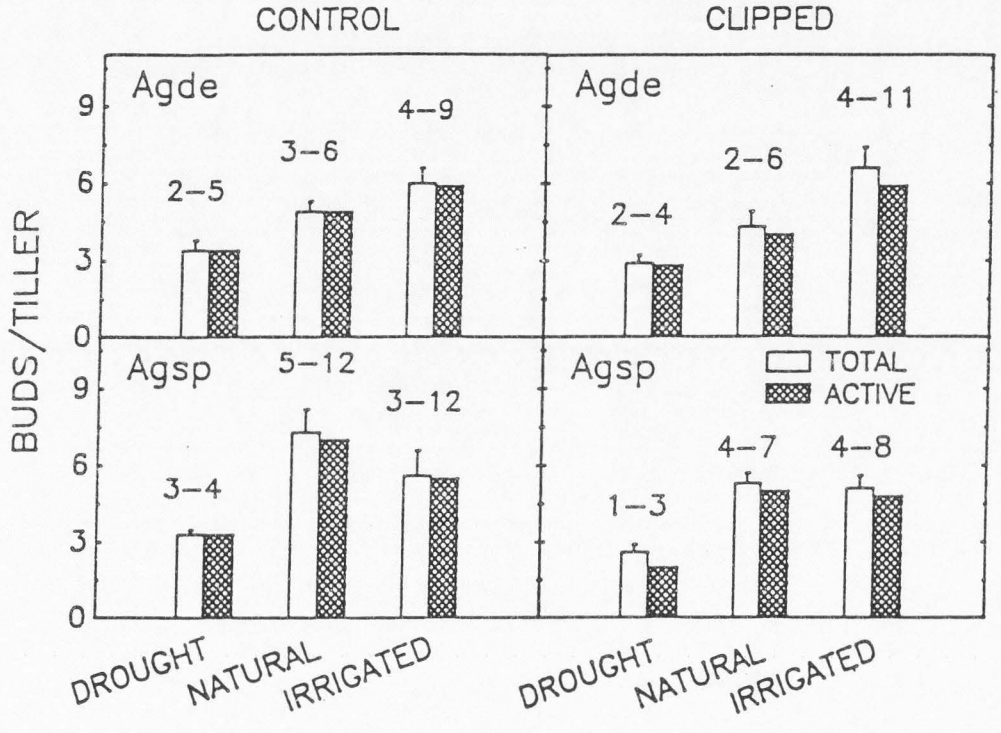


Fig. 14. Number of buds per tiller immediately after defoliation in 1986 of control and clipped plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural and irrigated conditions. Values shown are the total number of buds and the number of buds that stained with TTC (active). Each column is the mean ± SE of 7 or 8 tillers. Numbers above bars are the range in the total number of buds per tiller.

unclipped tillers of A. desertorum and A. spicatum subjected to natural conditions were within the range reported by Mueller and Richards (1986) for natural-exposed plants of both species. Less than 5 % of the total bud pool observed over all treatments in 1985 (n=256) and 1986 (n=452) showed no sign of respiratory activity. In both years, most (>71%) of the non-stained buds were from basal and mid-locations. There was little apparent influence of clipping on bud number or activity. However, clipped tillers on drought-treated A. spicatum plants had a lower number of metabolically active buds than unclipped ones (Fig. 14, $P < 0.05$).

Tiller buds of clipped and unclipped plants of both Agropyron species exposed to drought, natural and irrigated conditions exhibited a size gradient along the stem base (Mueller and Richards, 1986; Fig. 15). The upper and lowermost buds were the longest and shortest, respectively. Reduction in size from upper to lowermost buds varied from 43 to 89 %. Bud size of clipped plants of both species tended to be smaller than that of controls (e.g., distal buds on natural-exposed tillers in A. desertorum and on irrigated tillers in A. desertorum and A. spicatum; $P < 0.05$). Distal buds of unclipped tillers in A. spicatum were much shorter in the drought treatment than in the natural and irrigated treatments (Fig. 15, $P < 0.05$). In general, clipped and unclipped plants of A. spicatum had

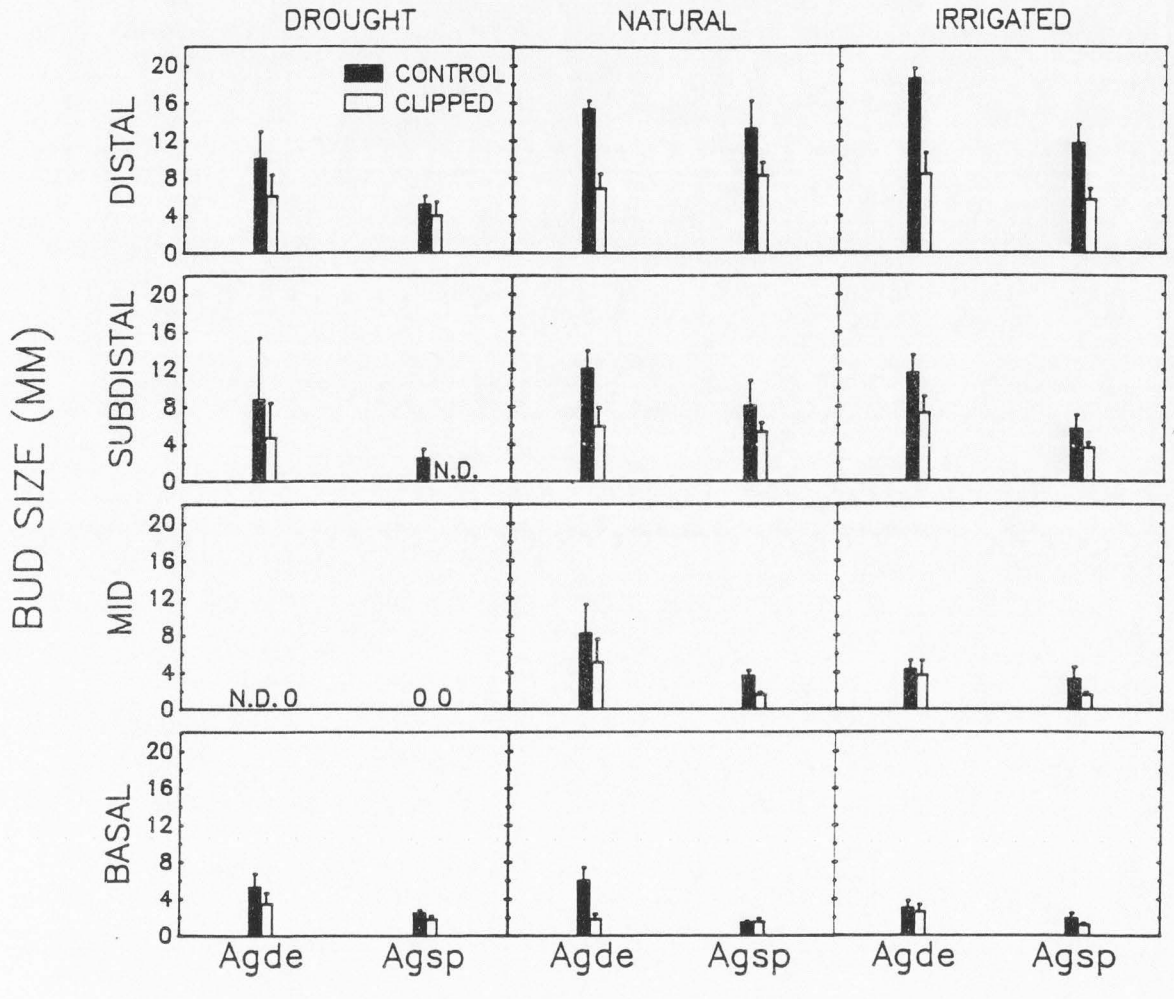


Fig. 15. Size variation of tiller buds immediately after defoliation in 1986 of control and clipped plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural and irrigated conditions. Buds were classified in distal, subdistal, mid or basal positions following Mueller and Richards (1986). Values are the means ± SE of between 4 and 16 buds; N.D.=not determined.

smaller buds than A. desertorum at comparable bud positions and water levels. Very few buds (18 of 452) from any of the treatments originated at positions on the culm above the basal cluster. Seventeen percent of these buds did not show respiratory activity, and 83 % were ≤ 9 mm.

Bud and Tiller Characteristics in Early Spring

The number and respiratory activity of buds on previous-year stems as well as tiller production and growth were determined from 2 to 4 weeks after snowmelt in early spring of 1986 and 1987. Determinations were made on plants of both species that had been either successively clipped once at the middle of each growing season since 1984 or left unclipped under the different water regimes.

In the early spring of 1986 two classes of previous-year stems were observed, each with quite different numbers of metabolically active axillary buds. One type produced one or more green tillers from their stem base buds, and this stem class had between 33 and 94 % (mean=80%) of their bud pool metabolically active (Fig. 16). Clipping and level of water availability only slightly affected either the total number or number of metabolically active buds observed on stems of this type. The second type of previous-year stems had no green tillers produced from buds formed the preceding year. These had only 6 to 33 % (mean=22%) of their bud pool metabolically active in 1986 and 1987 in the drought

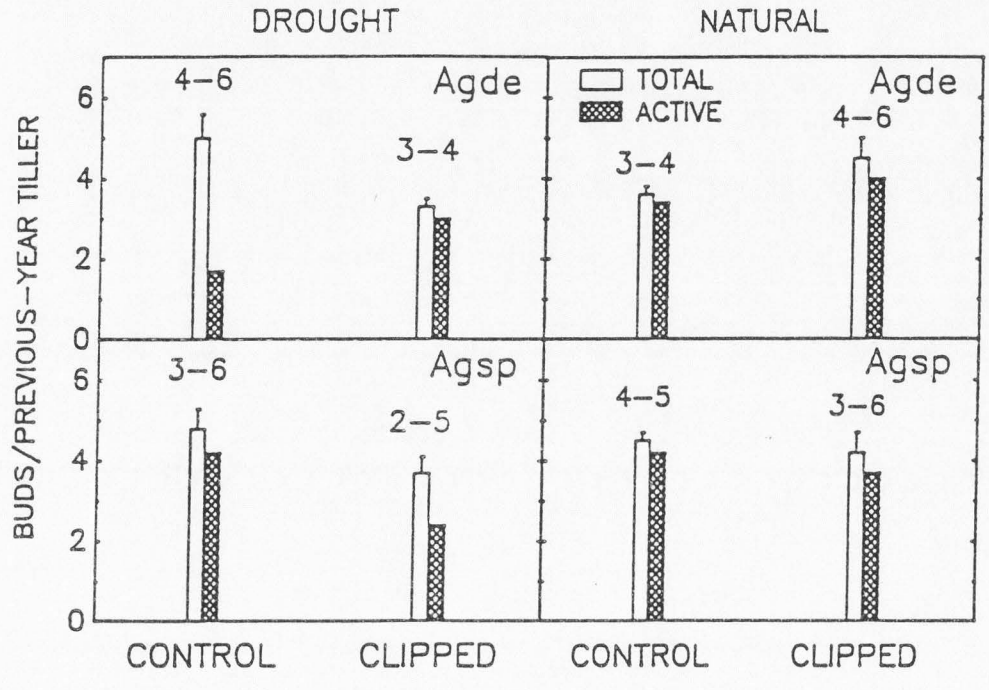


Fig. 16. Number of buds per previous-year tiller on control and clipped plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought or natural conditions. These stems had at least one green axillary tiller by the time they were sampled in early spring 1986. Values shown are the total number of buds and the number of buds that stained with TTC (active). Each column is the mean ± SE of between 3 and 7 tillers. Numbers above bars are the range in the total number of buds per tiller.

treatment. Even in the natural treatment in 1986, this stem class only had between 0 and 50 % (mean=17%) of the bud pool metabolically active. In 1986, a large proportion (40 to 70%) of the TTC-unstained bud pool was from basal positions in both types of previous year stems in the drought treatment. Fewer than 2 % of all observed buds (n=249) in 1986 were visually in an advanced stage of decomposition. These dead buds originated from mid and basal locations and were found on one-year-old stems of both species that did not have daughter tillers growing in early spring.

Control and clipped plants of A. desertorum and A. spicatum in drought and natural plots, and of A. spicatum in the irrigated plot, had similar tiller numbers and sizes in early spring 1985 after only one year of drought (data not shown). At this time, tiller numbers were lower on clipped than on unclipped plants of A. desertorum exposed to irrigated conditions. Because the number of green tillers was not counted in these irrigated-exposed plants of A. desertorum in 1984, it is not known whether this plant response was a treatment effect. In 1986, following 2 years of simulated drought or irrigation, tiller number and total leaf area were lower on clipped than on unclipped plants of both species (Fig. 17, $P < 0.05$). At this time, at least 56 % of the tillers on plants under all treatments originated from distal and subdistal bud locations. Similar to the pattern observed in 1986, a lower tiller number and total

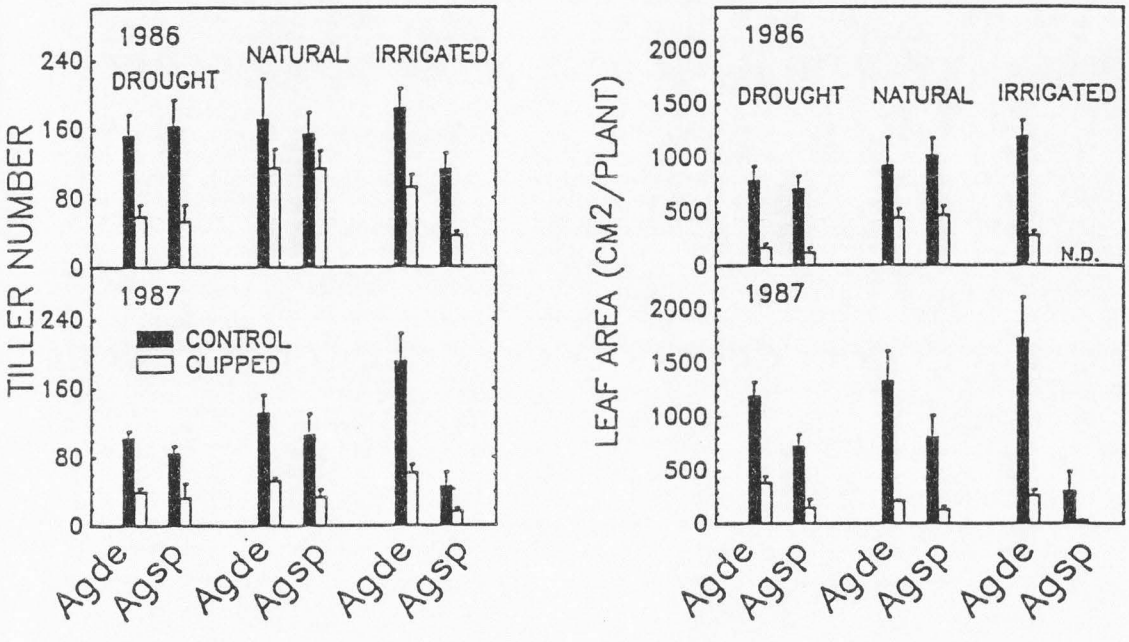


Fig. 17. Number of green tillers and green leaf blade plus stem and sheath surface area per plant in early spring 1986 and 1987 on control and clipped plants of A. desertorum (Agde) and A. spicatum (Agsp) exposed to drought, natural and irrigated conditions. Values are the means ± SE of between 3 and 8 plants; N.D.=not determined.

leaf surface area were observed in early spring 1987 on plants of A. desertorum ($P < 0.05$) and A. spicatum ($P \leq 0.08$) that had been successively clipped from 1984 than on controls under all water levels (Fig. 17).

Discussion

If intercalary and apical meristems are removed by grazing, a sufficient number of axillary buds must be activated and grow into tillers to replace a photosynthetic canopy. Any stress, such as drought, which reduces axillary bud number, activity and/or viability could then impose a constraint to regrowth immediately after defoliation. Grazing during culm elongation will often stimulate the growth of axillary tillers (Olson and Richards, 1988a). Although internode elongation was most likely occuring during the mid-May defoliation (Olson and Richards, 1988b) on the third year, almost no regrowth occurred on drought-exposed plants of either species. At this time, the number of axillary buds was lowest under water stress conditions on tillers of A. desertorum and A. spicatum (Fig. 14). These tillers grew out in early spring rather than in the previous autumn, which is the normal time for tiller growth of both species in the Great Basin (Mueller and Richards, 1986). As neither A. desertorum nor A. spicatum produced autumn tillers in the water stress treatment, they did not have overwintering leaves. Thus, drought-exposed tillers of

both species had fewer leaves and associated axillary buds at a comparable time during the growing season than those grown under higher water regimes (Fig. 14). The experimental drought imposed during the spring (1986) could also have contributed to their smaller bud number because primordium production (Husain and Aspinall, 1970) and bud differentiation and development (Olmsted, 1941; Brown, 1952; McIntyre, 1976) are very sensitive to water stress.

Most buds observed immediately after defoliation in 1985 and 1986 were metabolically active (Fig. 14). This is similar to results obtained by Johnson and Buchholtz (1962) with Agropyron repens and Heidemann and Van Riper (1967) with Panicum virgatum. A minimum of between 2 and 3 metabolically active buds were found on tillers of A. desertorum and A. spicatum immediately after clipping on the second and third year of successive defoliations. This active bud number, although low, would not itself limit the regrowth capacity of A. desertorum and A. spicatum following a defoliation event because these species usually produce only one or two daughters per parent tiller (Chapter IV; Mueller and Richards, 1986; Olson and Richards, 1988b).

After defoliation in 1986, the uppermost buds were generally smaller on clipped than on unclipped tillers of both species under all water levels (Fig. 15). This contrasts with the results of Mueller and Richards (1986) who found no bud length differences between clipped and

unclipped plants of these species. This difference may have resulted from repeated clipping of the plants in our study (1984 and 1985), while plants sampled by Mueller and Richards (1986) had not been previously clipped. Similar cumulative effects of repeated defoliation have been observed for Calamagrostis rubescens (Stout et al., 1980, 1981) and Danthonia caespitosa (Hodgkinson, 1976). The uppermost buds of clipped and unclipped tillers of A. desertorum and A. spicatum tended to be smaller under water stress than under higher moisture levels (Fig. 15). This could have been due to a decreased hydration of tissues which may limit bud growth (Olmsted, 1941; Gardner, 1942; McIntyre, 1976). Thus, immediately after two or more years of clipping under drought, the number and viability of the axillary buds on tillers of A. desertorum and A. spicatum did not limit the regrowth capacity of either species. The smaller bud size obtained in both species under drought conditions may delay regrowth somewhat. However, it is unlikely that this smaller bud size is a major constraint to regrowth following spring defoliation. This is because in our study as well as that of Mueller and Richards (1986) even the basal buds (the smallest within any given stem base, Fig. 15) produced tillers.

A. desertorum produced 2 times more tillers than A. spicatum about two weeks after defoliation under irrigated conditions in 1984 and 1985 (Fig. 13, Chapter IV). These

results are similar to those of Caldwell et al. (1981), Richards and Caldwell (1985) and Richards et al. (1988) in these species. The difference in tillering ability between A. desertorum and A. spicatum in 1985 occurred even though the number and viability of the axillary meristems were not a limiting factor for regrowth on either species. Similar results were obtained by Mueller and Richards (1986) in these tussock grasses. These authors also observed no differences in vascularization to basal- and mid-position buds in A. desertorum and A. spicatum, and refuted the possibility that bud growth could be physically constrained during its early growth by surrounding leaf sheaths in these species. Work of Richards and Caldwell (1985) further eliminated the possibility that crown carbohydrate availability could relate to the differential tillering ability of these bunchgrasses. Other factors that can affect bud outgrowth after defoliation include endogenous growth regulators, temperature, light quality and quantity and resource availability (i.e., water and nutrients) (Mitchell, 1953; Jewiss, 1972; Fletcher and Dale, 1974; Deregibus et al., 1983; Nus and Hodges, 1986). The importance of these factors as determinants of tillering needs to be investigated if we are to elucidate why A. desertorum produces more tillers than A. spicatum immediately following defoliation.

Regrowth from axillary buds usually occurs when grazing

removes intercalary and apical meristems. However, there are several situations where this type of regrowth does not occur. Spring regrowth did not occur under natural conditions when plants of A. desertorum were grazed after the completion of internode elongation (Olson and Richards, 1988a) nor did regrowth occur under drought in our study when defoliation was during (in 1986) or after (in 1985) culm elongation. In addition, normal fall tillering did not occur under drought conditions for either species in our study when these grasses were exposed to a dry autumn. Thus axillary buds produced prior to defoliation in one year constituted the bud pool for growth in the following spring.

At the beginning of spring in 1986 and 1987, previous-year stems with at least one green tiller had mostly metabolically active tiller buds. This suggests that when one bud grew out it allowed maintenance of other buds in the same stem base. Previous-year stems without a green tiller had mostly dead or dormant axillary meristems. Some of these buds may have undergone senescence by the end of the previous growing period (Mueller and Richards, 1986) while others either died during or remained dormant after the cold season, similar to the results of Haslam (1969) and Chalmers and Schmidt (1979). Tiller number, an indication of bud outgrowth, was lower on clipped than on unclipped plants of both species under drought or irrigation in early spring 1986, and under all water levels in early spring 1987 (Fig.

17). Water stress (McIntyre, 1976; Nus and Hodges, 1986; Jennane et al., 1987) and partial defoliation (Mitchell, 1953) can prevent bud outgrowth. Other studies (Neiland and Curtis, 1956; Stout et al., 1980, 1981; Hall et al., 1987) have also reported a decreased tiller production on grass species that have been severely and repeatedly clipped during one or more growing seasons.

In early spring 1987, when soil moisture was available to previously water-stressed plants, clipped tillers of both Agropyron species had a smaller green leaf surface area than unclipped ones (data not shown). Similar results were obtained at the same time in 1986 (data not shown). Rapid growth following release from water stress has been reported for several grasses (Hsiao et al., 1970; Hodgkinson, 1976; Wolf and Parrish, 1982). Following rewatering, however, clipped plants of A. desertorum and A. spicatum could not compensate for a reduced tiller number by enhancing growth of their tillers over that on unclipped controls. Our results are similar to those of Olson and Richards (1988b) in cattle-grazed or ungrazed plants of A. desertorum exposed to natural conditions. Amounts of green leaf surface area (Fig. 17) were therefore lower on clipped than on unclipped plants because they are related to both the number and size of vegetative tillers. The smaller leaf area on clipped plants of both species was caused more by a reduction in tiller number (mean=63%) than reduced tiller size

(mean=46%).

My results indicate that two or more periods of clipping under drought did not affect the regrowth capacity of these species immediately after spring defoliation. One year of clipping under a mild water stress did not reduce tiller number or size of the replacement tillers early in the following growing season. However, longer periods of drought and defoliation resulted in reduced tiller production in early spring, probably by causing inactivation of axillary meristems for regrowth. Because growth of these tillers was also diminished, this resulted in plants with a very reduced photosynthetic canopy. Continued grazing of these plants would reduce stand persistence and possibly allow invasion of less desirable species, thus contributing to a reduction in grass production.

CHAPTER VI

DROUGHT AND DEFOLIATION INTERACTION ON NONSTRUCTURAL CARBOHYDRATES AND EARLY SPRING GROWTH OF TWO COOL-SEASON GRASSES

Introduction

Soluble carbohydrates are important in initiating regrowth when a photosynthetic surface is nonexistent or when it is inadequate to maintain both respiration and growth demands (Heilmeier et al., 1986; Thorgeirsson, 1988). However, the role played by carbohydrate reserves in plant regrowth has been the subject of much controversy. From the analysis of carbohydrate concentrations only, many investigators (e.g. McIlvanie, 1942; Cook et al., 1958; Hyder and Sneva, 1959; Trlica and Cook, 1972 & Daer and Willard, 1981) concluded that reserve carbohydrates have a fundamental role in plant regrowth. When absolute quantities as well as concentrations were taken into account, however, completely different conclusions have been drawn. For example, Richards and Caldwell (1985) demonstrated that crown carbohydrate concentrations or pools were not related to regrowth rate or production in Agropyron desertorum and Agropyron spicatum*. Limited availability of actively growing meristems were more important than carbohydrate availability in these experiments. However, in early spring when intercalary and apical meristems are present on growing

tillers of these species, carbohydrate concentrations or pools may limit regrowth rate or production of these or other pasture grasses.

Range plants are often grazed under conditions of drought stress (Ludlow, 1986). Carbohydrates could accumulate in crowns and roots of these plants (Brown and Blaser, 1965; Whalley and Davidson, 1969; Dina and Klikoff, 1973; Deregibus et al., 1982) because growth is impaired before photosynthesis under water stress (Wardlaw, 1969; Boyer, 1970; Hsiao, 1973). If so, and if carbohydrate concentrations or pools were important determinants of early spring growth, defoliation under drought in the preceding year/s could have a significant impact on plant recovery after alleviation of these stresses.

This chapter reports a study of the relationship between the availability of crown or root soluble carbohydrates and early spring growth in two cool-season grasses, A. desertorum and A. spicatum. These species were selected because they are an important forage resource in the rangelands of the Intermountain West (Dewey and Asay, 1975; West, 1983) and differ greatly in tolerance of grazing (Hyder and Sneva, 1963; Caldwell et al., 1981). The grazing-tolerant species, A. desertorum, was introduced from Eurasia while the grazing-intolerant species, A. spicatum, is native to the Intermountain West. The specific objective was to determine the relationship between crown and root total

nonstructural carbohydrate (TNC) concentrations or pools and early spring growth on field-grown plants of A. desertorum and A. spicatum that had been exposed to drought or to the combination of drought and defoliation during one or more years.

Materials and Methods

Dark Regrowth Experiments

The etiolated regrowth technique (McKendrick and Sharp, 1970; Richards and Caldwell, 1985) was used to examine the relationship between soluble carbohydrates and early spring growth without confoundment of carbon input from photosynthesis.

Plants of both grass species were excavated from each water and defoliation treatment plot at the beginning of each etiolated regrowth experiment in 1985 and 1986. The excavated plants provided estimates of initial crown and root TNC concentrations. They could not be used to provide initial TNC pool estimates because they were smaller than plants utilized in the etiolated regrowth studies. Three plants per treatment were harvested for this purpose from 17 to 21 May in 1985 and from 28 March to 5 April in 1986.

Total number of tillers was counted on each plant and the aboveground material was then separated into shoots and crowns, which included the lowest 1 cm of stem base and 1 cm of attached roots. The crowns were washed free of soil.

Roots were obtained from a 4 dm^3 soil block and from 6 soil cores (0.16 dm^3 each) taken at predefined soil depths and distances from the plant center (Fig. 28 in Appendix). Roots were washed free of soil with a root washing machine (Smucker et al., 1982). After washing, sagebrush roots and debris were removed manually. Shoot, crown and root samples for TNC determinations were frozen immediately after harvest and then freeze-dried and weighed. All materials were then ground to pass a 40-mesh screen for carbohydrate analysis.

Dark regrowth experiments were initiated on 28 May in 1985 and on 19 April in 1986, as soon as weather allowed after the initial harvests were completed. In 1985, apical meristem height was determined on a large number of tillers of varying height. These data were used to determine appropriate harvest height so that leaf blades and green stem and sheaths above approximately 90 % of all apical meristems were removed. All remaining leaf blades were individually cut above their corresponding intercalary meristems. In 1986, only leaf blades were individually removed from the tillers at the initiation of the dark regrowth experiment. Subsequently, each plant was covered with a 50x50x60 cm cardboard box wrapped with plastic on the inside and aluminum foil on the outside. Aluminum foil was used to reduce heating. Leaf blades produced in the dark were harvested at frequent intervals (6 to 10 days) until growth ceased. This procedure eliminated meristematic

limitations on growing tillers of both species because active intercalary and apical meristems remained after harvesting of leaf blades. Each year at the end of the experiment all 36 plants (12 treatments, 3 plants per treatment) were harvested using the destructive harvesting procedure already described (Fig. 28 in Appendix). Shoots were separated into upper leaf stem and sheaths (as produced in dark) and lower stem and sheaths (as remained after dark regrowth initiation). All harvested plant materials were freeze-dried, weighed and ground for TNC analysis.

It was assumed that crown and root biomasses of dark-grown plants represented 55 % of initial biomasses on both species. This figure was obtained from Table 1 in Richards and Caldwell (1985) by calculating crown biomass losses for each species on all etiolated regrowth experiments that they conducted. Values calculated for both species were pooled because they were not statistically different (Mann-Whitney U-Test; $P>0.05$). TNC pools were calculated by multiplying the estimated total dry weight of the organ (initial biomass=final biomass/0.55) by its carbohydrate concentration (dry weight basis).

The Mann-Whitney U-Test (Zar, 1984) was utilized to assess statistical differences among treatments.

Total Nonstructural Carbohydrate Analysis

Total nonstructural carbohydrates were determined as

described by Chatterton et al. (1986). Tissue samples (50 mg) were digested with amylase (Clarase 40,000) for 24 h at 38 C. Enzyme digests were then hydrolyzed with 0.6 N HCl. The TNC fraction reported in this paper thus includes glucose, fructose, sucrose, and both soluble and insoluble starch and fructans. Reducing sugar determinations were made by employing a Technicon Autoanalyzer II. Roots proximal to the stem bases (soil block roots) were treated separately from more distal roots (soil core roots) in the determination of TNC. Soil cores were taken between 17.5 and 32.5 cm from the plant center (see Fig. 28 in Appendix). Total nonstructural carbohydrate concentrations were usually from 40 to 380 % greater on roots obtained from the soil blocks than on more distal roots extracted from the soil cores. A weighted average between roots of the soil block and roots of the soil cores is reported.

Results

The importance of carbohydrate availability in crowns and roots in determining early spring growth was evaluated by obtaining data on biomass and TNC concentrations of these organs. TNC concentrations or calculated pools (biomass x concentration) were then related to the production of etiolated regrowth.

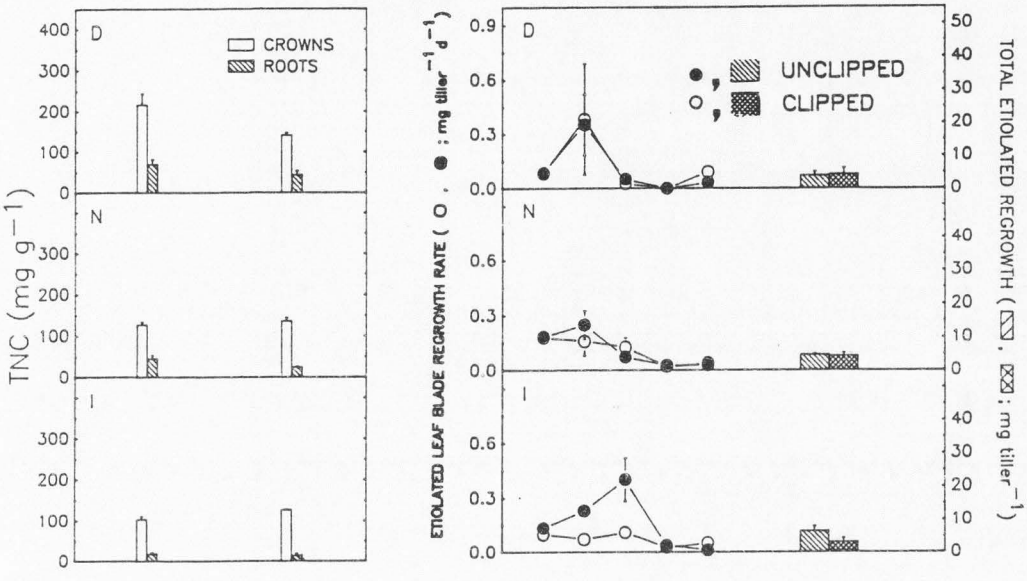
Total Nonstructural Carbohydrates

Concentrations

Early spring shoot (100 to 250 mg g^{-1}), crown and root TNC concentrations were similar between clipped and unclipped plants of A. desertorum and A. spicatum in 1985 (Fig. 18) and 1986 (Fig. 19). In both years, however, clipped plants of A. spicatum had lower crown TNC concentrations than unclipped controls under drought conditions ($P=0.08$). Similarly, root TNC concentrations were lower in 1985 and 1986 on clipped than unclipped plants of A. spicatum exposed to natural conditions ($P=0.08$). A. desertorum showed greater initial shoot (data not shown) and crown TNC concentrations than A. spicatum in 1985 (Fig. 18) and 1986 (Fig. 19). The two species did not differ, however, in their root TNC concentrations in either year. Initial concentrations of TNC in crowns and roots were similar or greater in the drought than in the natural or irrigated treatments in 1985 and 1986 for both species. In both years, initial crown TNC concentrations were from 6 to 29 times greater than those in roots in A. desertorum and from 2 to 9 times greater than those in roots in A. spicatum.

As expected, crown carbohydrate concentrations were reduced during the dark regrowth experiments. After regrowth ceased, crown TNC concentrations measured on all treatments represented between 14 and 84 % in 1985, and between 5 and

Agsp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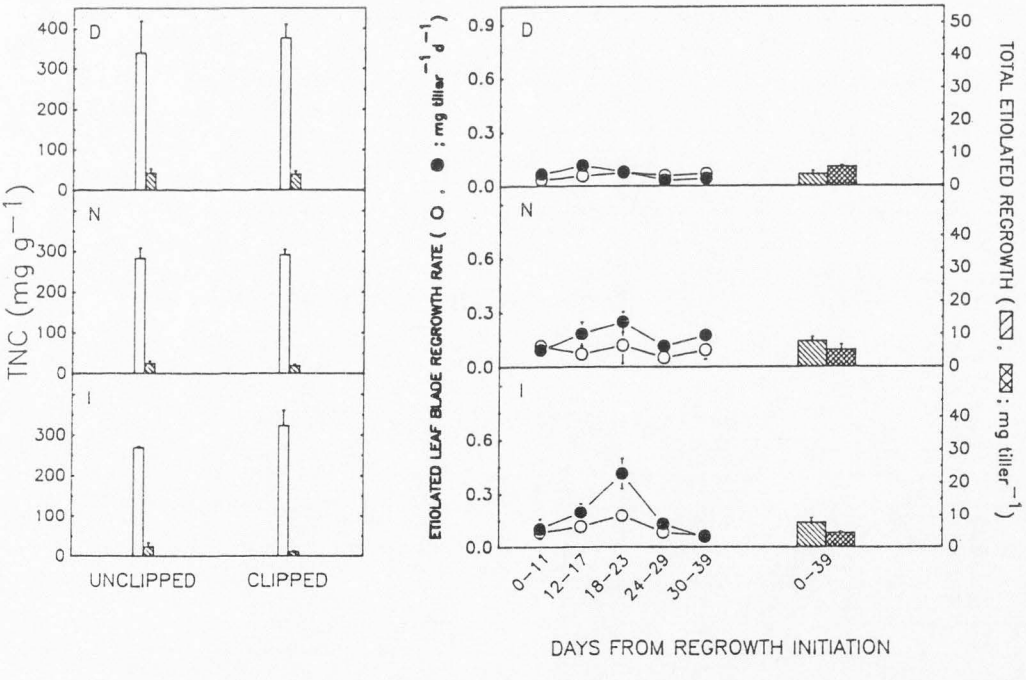
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24–29
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DAYS FROM REGROWTH INITIATION

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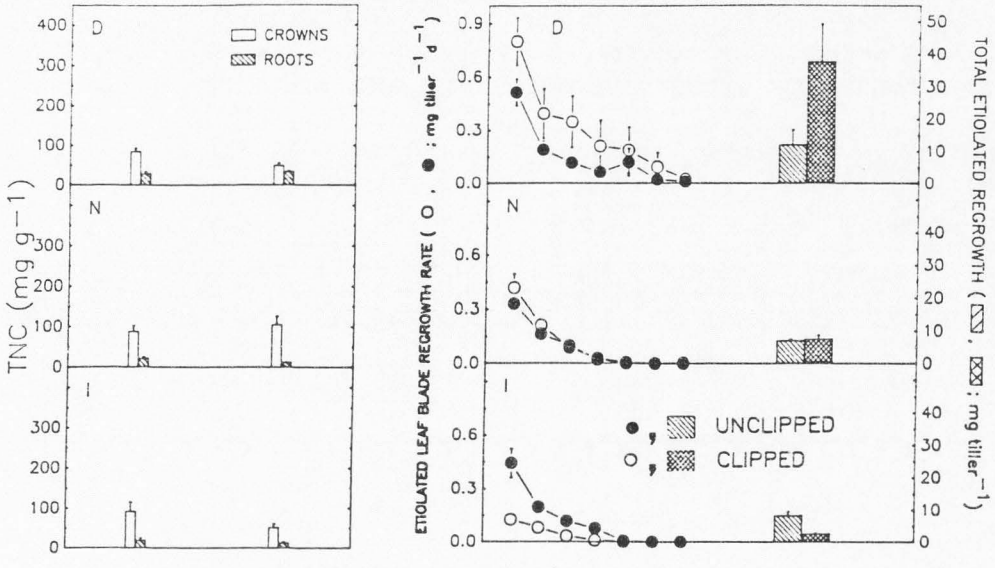
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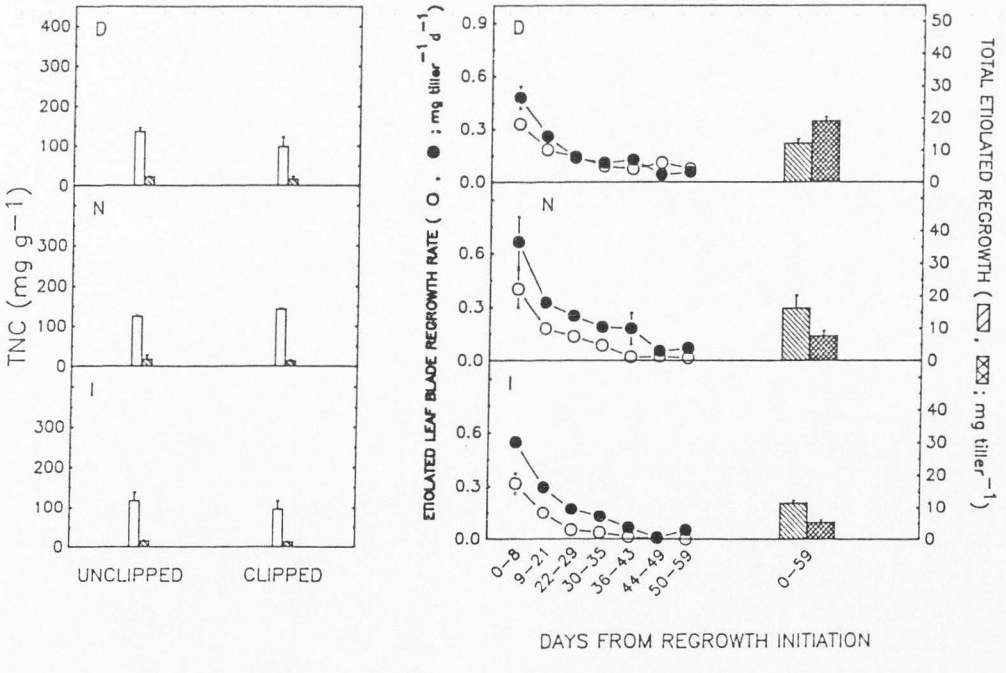
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9–21
22–29
30–35
36–43
44–49
50–59
0–59
DAYS FROM REGROWTH INITIATION

23 % of initial values in 1986. Final root TNC concentrations were from 24 to 70 % lower than initial values for all treatments in 1986.

Pools

One year after a severe defoliation, crown and root TNC pools were similar between clipped and unclipped tillers of A. desertorum and A. spicatum in the drought and irrigated plots (Fig. 20). However, crown TNC pools in A. desertorum, and root TNC pools in both species were lower in clipped than in unclipped tillers under natural conditions. At this time, A. desertorum had greater crown TNC pools than A. spicatum at all water levels. The two species had similar total (crowns plus roots) pools of TNC, because root TNC pools were slightly higher in A. spicatum than in A. desertorum. In 1986, initial TNC pools in crowns and roots did not differ significantly between clipping treatments and species (Fig. 21). However, under drought conditions crown and root TNC pools were apparently greater in clipped than in unclipped tillers of both species.

Crown TNC pools were usually greater under drought than under better moisture levels for clipped and unclipped tillers of both species in 1985 (Fig. 20) and 1986 (Fig. 21). This was mostly the result of greater crown biomass in the drought treatment (data not shown). Root biomass was similar or lower under drought than under natural or irrigated conditions in both years (data not shown).

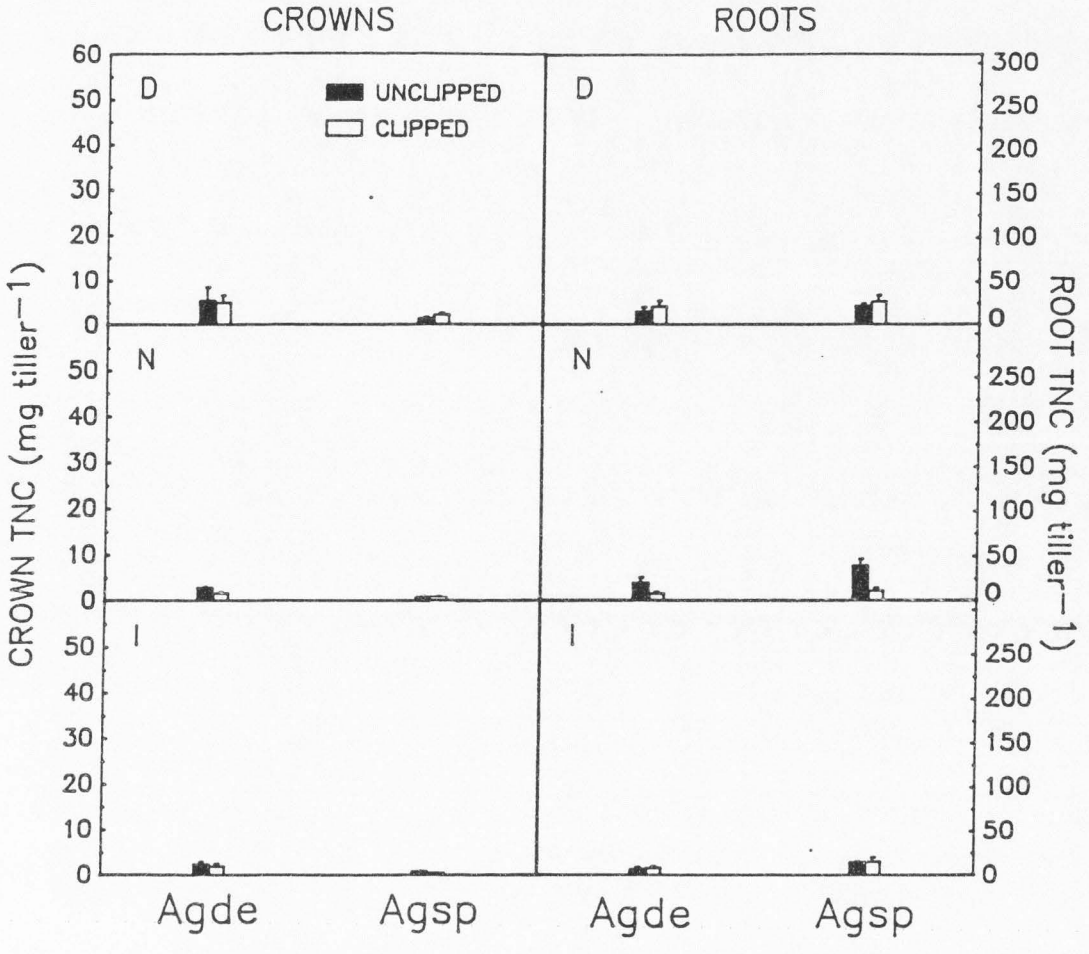

Fig. 20. Crown or root TNC pools in plants of A. desertorum (Agde) and A. spicatum (Agsp) in mid-May 1985 just prior to (or at) the initiation of the etiolated regrowth experiments. These plants had been clipped or left unclipped under drought (D), natural (N) or irrigated (I) conditions since 1984. Each bar is the mean (± SE) of 3 plants. Compare to Fig. 21 for 1986 data on same scale.

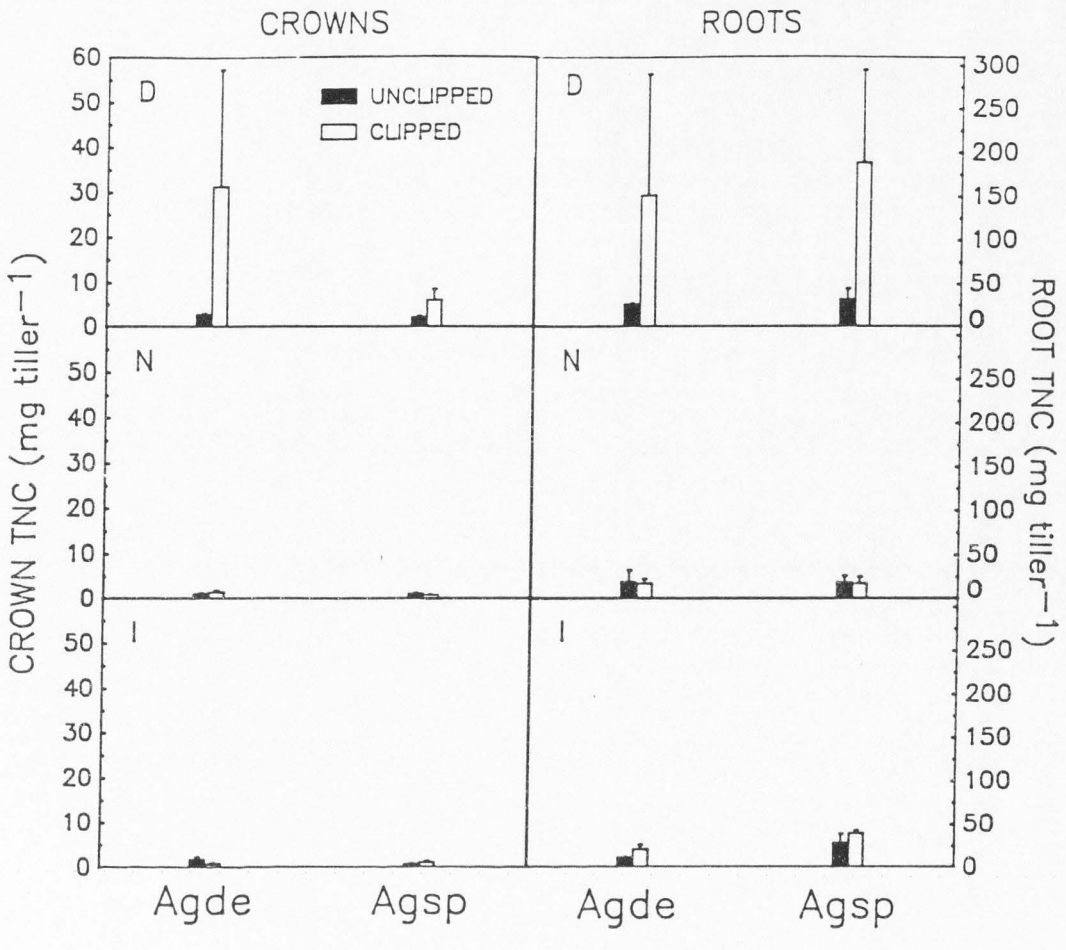

Fig. 21. Crown or root TNC pools in plants of A. desertorum (Agde) and A. spicatum (Agsp) in late March-early April 1986 just prior to (or at) the initiation of the etiolated regrowth experiments. These plants had been clipped or left unclipped under drought (D), natural (N) or irrigated (I) conditions since 1984. Each bar is the mean (± SE) of 3 plants. Compare to Fig. 20 for 1985 data on same scale.

However, root TNC pools were similar or greater under drought than under better moisture regimes because root TNC concentrations were higher in drought- than in natural- or irrigated-exposed tillers of both species. The greatest crown and total TNC pools in 1986 were found in clipped and drought-treated tillers of both species.

Early spring crown or root biomass of drought-exposed tillers of A. desertorum and A. spicatum was more than 6.3 times higher in 1986 than in 1985. However, crown or root TNC concentrations of these tillers were on average more than 1.9 times greater in 1985 than in 1986. The net effect was that early spring crown and root TNC pools in the drought treatment were on average more than 2.7 times greater on the third (1986) than on the second (1985) year of successive treatments.

Crowns of both species contained between 4 and 12 % of the total (shoot plus crown plus root) plant carbohydrate pools measured in early spring of 1985 and 1986. These crown TNC pools were from 2 to 5 times lower than those measured for shoots.

Production of Etiolated Regrowth

Consistent with the results of Richards and Caldwell (1985) for these species, initial regrowth was much faster in both species when it occurred earlier (i.e., in 1986, Fig. 19) than later (i.e., in 1985, Fig. 18) in spring.

The average rate of production of leaf blades on clipped tillers of A. spicatum, and to a lesser extent on clipped tillers of A. desertorum, was greatest in the drought treatment in 1986. Both species also produced leaf stem plus sheath (more than 50 % of total production) at a rate greater than that of blades under these conditions. Clipped and natural- or irrigated-exposed tillers of both species produced mostly leaf blades (88 to 100 % of total production). Therefore, clipped tillers of A. desertorum and A. spicatum produced more total etiolated regrowth in the drought plot than in the natural or irrigated plots (Fig. 19; P=0.08). On the other hand, the average rate of leaf blade production and the total amount of etiolated regrowth of unclipped tillers of both species were similar at all water levels.

Unclipped tillers of A. desertorum consistently produced more etiolated regrowth than those of A. spicatum in 1985 (Fig. 18) and 1986 (Fig. 19) under natural conditions (P=0.08 in both years).

Relationship between Carbohydrate Availability and Growth in Early Spring

Within a water level, initial crown and root TNC concentrations of clipped and unclipped plants of both species did not relate to regrowth rate and total production of etiolated regrowth in 1985 (Fig. 18) and 1986 (Fig. 19). For example, regrowth rates and total production of

etiolated regrowth were greater at lower than higher crown TNC concentrations (Fig. 19, D, A. spicatum) and vice versa (Fig. 19, N, A. desertorum). Similarly, high TNC concentrations in roots produced similar regrowth rates and total amount of regrowth as low TNC concentrations in the same organ (Fig. 19, N, A. spicatum). Also, rates of regrowth and/or total growth production were higher on unclipped than on clipped tillers of both species (Figs. 19, I, A. spicatum and 19, N and I, A. desertorum) or vice versa (Fig. 19, D, A. spicatum and A. desertorum) even though they had similar root TNC concentrations.

The degree of TNC depletion after growth ceased in 1985 and 1986 did not relate to the amount of etiolated growth produced by clipped or unclipped tillers. For example, the decline in crown (~85%) or root (~50%) TNC concentrations was similar for clipped and unclipped tillers of A. spicatum exposed to irrigated conditions in 1986. However, the total dark regrowth production was about 3 times higher for unclipped than for clipped tillers of this species (Fig. 19, I).

Initial crown and root TNC concentrations in A. desertorum and A. spicatum did not relate to etiolated regrowth rate (not shown) or total production (Fig. 22) when the relationship was constructed to compare among water and defoliation treatments in 1985 and 1986. A positive relationship, however, was suggested between root TNC

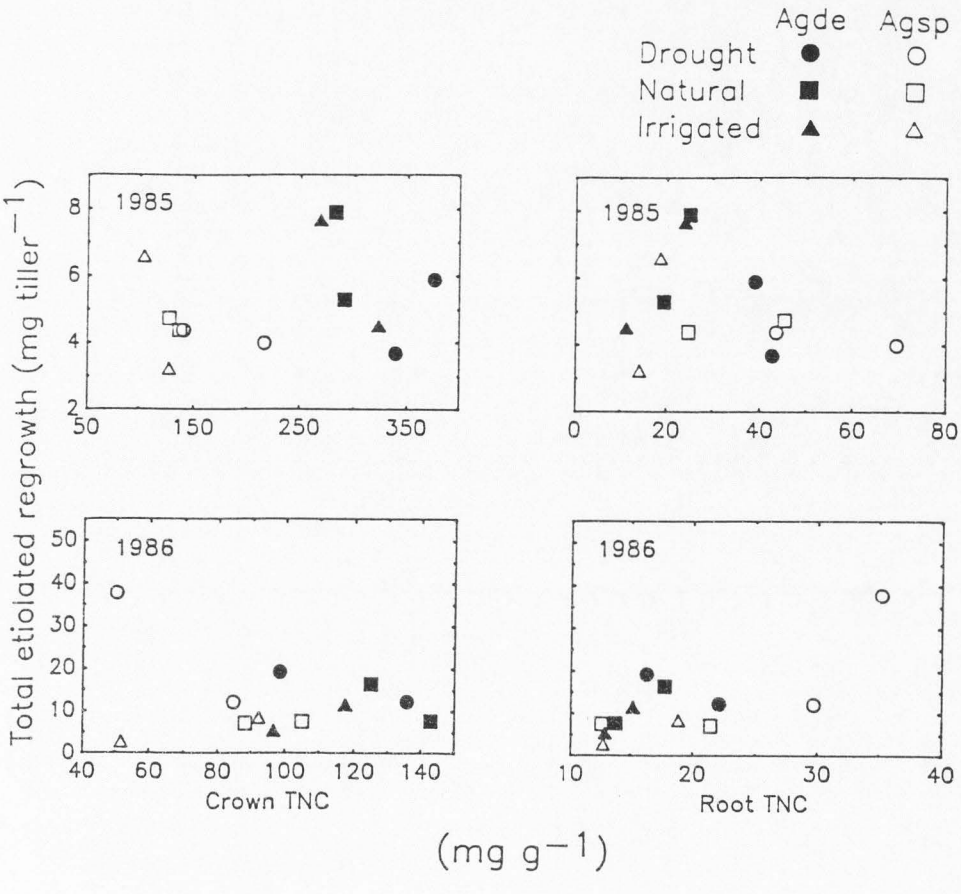

Fig.22. Relationship between initial crown or root TNC concentrations and total production (blade plus stem and sheaths) of etiolated regrowth for the dark regrowth experiments conducted in 1985 and 1986 on plants of A. desertorum (Agde, closed symbols) and A. spicatum (Agsp, open symbols) that had been clipped or left unclipped under drought, natural or irrigated conditions since 1984. Each symbol is the mean of 3 plants.

concentrations and total production of etiolated regrowth in A. spicatum in 1986.

In 1985, there was no relationship between the estimated pool of TNC in crowns or crowns plus roots and the rate (not shown) or total amount of etiolated regrowth produced by A. desertorum and A. spicatum at all water levels (Fig. 23). However, when a wider range of TNC pools was obtained, a positive relationship was obtained for both species between crown or total TNC pools and total production of etiolated regrowth in 1986.

Discussion

Much research has reported the effect of defoliation on crown or root nonstructural carbohydrates of these Agropyron species (i.e., McIlvanie, 1942; Cook et al., 1958; Garrison, 1966; Caldwell et al., 1981). In this study, crown TNC pools in A. desertorum and root TNC pools in A. desertorum and A. spicatum were lower for clipped than for unclipped tillers one year after a severe defoliation under natural conditions (Fig. 20). These findings are in accord with those of Cook et al. (1958) and Caldwell et al. (1981) for these species. At the same time, however, no clipping effect was detected on crown or root TNC pools for both species in the drought and irrigated treatments. Also, crown or root TNC concentrations, in 1985 (Fig. 18) and 1986 (Fig. 19), and pools, in 1986 (Fig. 21), were similar between

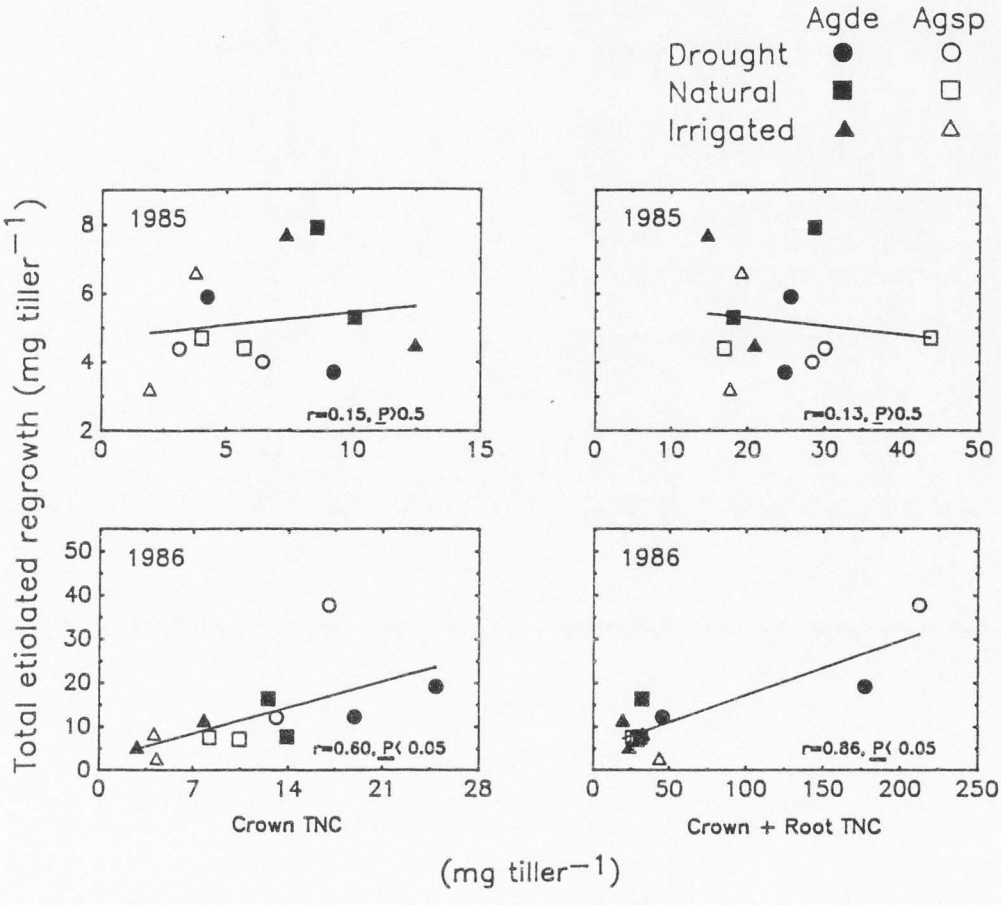

Fig. 23. Estimated initial crown or total (crown plus roots) pools of TNC against total production (blade plus stem and sheaths) of etiolated regrowth in the dark regrowth experiments conducted in 1985 and 1986 on plants of A. desertorum (Agde, closed symbols) and A. spicatum (Agsp, open symbols) that had been clipped or left unclipped under drought, natural or irrigated conditions since 1984. Each symbol is the mean of 3 plants. A single regression line was fitted for both A. desertorum and A. spicatum since separate linear regressions for each species were not significantly different at $P<0.05$.

clipping treatments under all water levels for both species. This lack of clipping effect may have been the result of the late defoliation treatments in 1984 (29 June) and 1985 (13 June). However, it could also be due to expressing carbohydrate pools on a per tiller basis. For example, in 1986 (but not in 1985) tiller number was lower on clipped than on unclipped plants of both species under all water regimes (Chapter V). Other studies have also indicated little or no change in crown or root nonstructural carbohydrate concentrations or pools following one or more years of defoliation (Jameson and Huss, 1959; Buwai and Trlica, 1977 a&b; Menke and Trlica, 1983; Christiansen and Svejcar, 1987).

It is well established that water stress can depress growth relatively more than net photosynthesis (Wardlaw, 1969; Boyer, 1970; Hsiao, 1973) and that when this occurs carbohydrates can accumulate in plant tissues (Brown and Blaser, 1965; Whalley and Davidson, 1969; Deregibus et al., 1982). In agreement with this view, crown or root TNC concentration and pools were similar or higher, but not lower, under drought than under irrigated conditions in both species. These results are similar to those reported by Trlica and Cook (1972) for Agropyron desertorum and by Brown and Blaser (1965), Blaser et al. (1966), Whalley and Davidson (1969), Pettit and Fagan (1974) and Drossopoulos et al. (1987) for other grasses.

In the two dark regrowth studies, the amount of etiolated regrowth produced under natural conditions was greater in unclipped tillers of A. desertorum than in those of A. spicatum (Figs. 18 and 19). This result is similar to that of Richards and Caldwell (1985) for these species; these authors attributed this response to a greater efficiency of A. desertorum in producing new foliage from stored reserves or a greater proportional allocation of mobilized compounds to regrowing shoot meristems for this species. Regrowth in the light is also greater for A. desertorum than for A. spicatum (Cook et al., 1958; Caldwell et al., 1981).

Shoot, crown and root TNC concentration and pools found in this study for A. desertorum and A. spicatum are comparable to values previously reported for these species (Cook et al., 1958; Trlica and Cook, 1972; Caldwell et al., 1981; Daer and Willard, 1981; Richards and Caldwell, 1985; Chatterton et al., 1986). Concentrations of TNC in crowns or roots, however, were inadequate indicators of regrowth production in early spring; etiolated regrowth rate and total production on these species were high when crown TNC concentrations were low (i.e., Fig. 19, D, A. spicatum) and vice versa (i.e., Fig. 19, N, A. desertorum) or they were similar at different root TNC concentrations (i.e., Fig. 19, N, A. spicatum). These results are in agreement with those of Richards and Caldwell (1985) for these species and of

Sheard (1968) for Phleum pratense. They disagree, however, with previous studies for these (Trlica and Cook, 1972; Daer and Willard, 1981) and other pasture grasses (Ward and Blaser, 1961; Agdegbola and McKell, 1966; Coyne and Cook, 1970; Menke and Trlica, 1981), which reported that TNC concentrations in crowns or roots were important determinants of growth in early spring.

Similar to concentrations, crown or total TNC pools in A. desertorum and A. spicatum were not associated to growth in mid-spring of 1985 (Fig. 23). These results are similar to those of Richards and Caldwell (1985) in these species when growth was limited by the availability of intercalary and apical meristems after plants had been severely clipped in May, June or July. In early spring of the following year (1986), however, higher pools than those in 1985 were obtained; under these circumstances TNC pools in crowns or crowns plus roots and early spring growth appeared associated. These results are similar to those obtained for other pasture grasses when their growth was not limited by the availability of actively growing meristems and conditions were conducive to rapid growth (Agdegbola, 1966; Bommer, 1966). The difference between the results obtained in 1985 and 1986 may be due to several factors. Meristematic tissues were probably less active in 1985 than in 1986 because the 1985 experiment was initiated 39 days later than that in 1986. Some apical (~10%) and leaf blade intercalary

meristems were removed at the initiation of the study in 1985, while only leaf laminae above their intercalary meristems were harvested during the experiment in 1986. Additionally, plants of both species were exposed to greater water stress conditions during the experiment in 1985 than in 1986 (see Figs. 1 and 2). The range in crown or total TNC pools was also smaller in 1985 than in 1986. This was the result of the high amounts of carbohydrates that accumulated in storage organs of plants that had been exposed to drought or to the combination of drought plus defoliation during two consecutive years. The greater water stress conditions in 1985 than in 1984 (see Figs. 1 and 2) probably caused the higher crown or total TNC pools on drought-exposed plants in 1986 than in 1985.

The results of the study in 1986 suggest that accumulation of high amounts of TNC in storage organs of drought-exposed plants (i.e., Fig. 23) could lead to rapid plant recovery upon release from water stress in early spring. This is a time when there is no meristematic limitations on growing tillers. In early spring 1987, when moisture was available at all water level plots, leaf area was usually greater for tillers of both species that had been exposed to water stress in the previous years than for those grown under better moisture levels (data not shown). Rapid growth after release from water stress (Hsiao et al., 1970; Hodgkinson, 1976; Wolf and Parrish, 1982) or the

combination of water stress and defoliation (Hodgkinson, 1976) has been previously observed for other perennial grasses. The contribution of carbon reserves to shoot regrowth in early spring, however, would probably exceed that from photosynthesis for only a few days (Richards and Caldwell, 1985; Heilmeier et al., 1986).

In this study, crown or root TNC concentrations were poor indicators of etiolated growth production in early spring. However, crown or total TNC pools and early spring growth appeared positively associated when high amounts of TNC accumulated in the storage organs of drought-exposed plants. These TNC pools, however, were estimated rather than measured. Also, the production of etiolated regrowth in the drought plot took place under a substantial soil water deficit in 1986 (see Fig. 1). Thus, the relationship between a wide range of crown or total TNC pools and regrowth production needs to be tested under conditions more similar to those found in early spring, when not only intercalary and apical meristems on growing tillers but also water and nutrients do not limit regrowth.

CHAPTER VII

SYNTHESIS

Previous studies of the influence of defoliation and water stresses on plant growth face several problems: they have looked at the separate effects of defoliation and water stresses, have been conducted under greenhouse or growth chamber conditions, have not adequately measured levels of both stresses, have not included control plants and/or have determined plant responses only by end-of-season harvests of standing crop without trying to understand why those responses occurred. I attempted to address these limitations in the present study. This makes it possible to better predict the effects of one or more years of late and severe utilization of A. desertorum and A. spicatum under drought conditions.

The productive potentials of A. desertorum and A. spicatum were not affected after plants of these species were severely defoliated (after internode elongation) under mild water stress (i.e., 1984). On the third year of repeated treatments, however, the reestablishment of a green canopy in A. desertorum and A. spicatum was severely reduced immediately following defoliation during drought. This was associated with reductions in leaf extension rates, production of new tillers, rate of production of new leaves, height growth and duration of growth, which resulted in very low shoot yields in both species. At the same time, the

number (2 or 3) and size of the axillary buds on tillers of both species was lowest in the drought treatment. Most of these buds, however, were metabolically active. Thus, regrowth capacity immediately after defoliation during drought was not limited by bud number, size or viability. This is because tillers of these species usually produce only one or two daughters, and even the smallest buds within any stem base are capable of producing tillers (Mueller and Richards, 1986).

After 2 successive years of drought or defoliation during drought, total nonstructural carbohydrates (TNC) rose to high levels in crowns and roots of both species. This result indicates that regrowth of these species in early spring would most likely not be limited by carbohydrate availability after repeated periods of drought or drought plus defoliation. Within each species, the greatest production of etiolated regrowth was produced on clipped and drought-treated tillers in early spring of 1986. These tillers had also the largest crown or total pools of TNC. These results suggest that plants exposed to prolonged periods of drought and grazing may have rapid tiller growth upon alleviation from these stresses in early spring if high amounts of TNC were accumulated in their storage organs during the stress period/s. This enhanced tiller growth, however, could be offset by a reduced tiller production on these plants. For example, tiller number was lower for

clipped than for unclipped plants of both species under drought conditions in early spring 1986 and 1987. This reduced tiller production on clipped plants did not relate to levels of carbohydrate reserves in crowns or roots but was probably caused by a lack of metabolic activity of the replacement axillary buds. In early spring of the third year of repeated treatments, tillers of clipped and drought-treated plants of both species also showed the lowest rates of new leaf production, total green leaf areas, and shoot yields. The reduced tiller production and tiller growth severely restricted the recovery of both species in early spring after 2 years of drought plus defoliation.

Continued utilization of these species after 2 or more years of drought would most likely reduce the persistence of these grasses in the community and possibly allow invasion of less desirable species. Ultimately, this would contribute to a reduction in grass production and diminish rangeland carrying capacity. If the range manager had to face 2 or more consecutive dry years, he could allow late grazing of these grasses but should plan on their reseeding later on. Future efforts on the effects of earlier and/or less severe defoliations (than those used in this study) are neccesary to provide information in grazing management of these species under drought in a way that assures their persistence in the community.

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APPENDIX

1984

SOURCE OF VARIATION	df	MEAN SQUARES							
		NGL	TH	BL	SSHL	TOTL	BA	SSHA	TOTA
REPLICATES	1	0.01	312.94	1.76	336.83	387.67	9.80	12.64	44.82
WATER	1	0.08	13.64	0.08	92.09	93.30	0.08	3.44	2.48
CLIPPING	1	173.10**	20175.38***	7099.85**	11916.40**	37277.47**	304.52*	448.46**	1492.42**
WATERxCLIPPING	1	0.14	8.53	6.71	230.40	328.26	0.19	8.66	11.45
ERROR A	3	2.90	87.51	146.20	242.85	742.54	19.85	9.13	55.48
SPECIES	1	1.93	53.22	381.78	607.30*	22.54	90.40	22.86*	22.34
WATERxSPECIES	1	0.14	74.51	8.21	107.95	185.19	1.78	4.06	11.25
CLIPPINGxSPECIES	1	0.08	39.78	227.54	221.16	0.31	30.47	8.32	6.96
WATERxCLIPPINGxSPECIES	1	0.36	75.89	4.28	103.30	158.46	0.31	3.88	6.43
ERROR B	4	0.86	101.57	87.91	51.78	232.88	12.97	1.94	19.20
DATES	7	29.27***	326.13***	2794.75***	353.49***	5045.05***	165.09***	13.31***	267.89***
WATERxDATES	7	0.43**	6.90	28.64*	25.42***	94.52***	4.02	0.96***	8.80*
CLIPPINGxDATES	7	13.00***	395.15***	813.49***	234.31***	1721.37***	47.19***	8.81***	79.73***
SPECIESxDATES	7	1.53***	18.33***	18.71	7.36	33.13	11.52**	0.28	14.64***
WATERxCLIPPINGxDATES	7	0.30*	7.23	15.96	2.50	25.81	0.90	0.09	1.31
WATERxSPECIESxDATES	7	0.09	3.59	3.71	7.99	14.46	1.58	0.30	1.39
CLIPPINGxSPECIESxDATES	7	0.91***	10.32	13.84	31.51***	20.09	3.52	1.18***	5.85
WATERxCLIPPINGxSPECIESxDATES	7	0.17	3.97	9.78	10.94	33.29	1.41	0.41	2.98
ERROR C	56	0.12	3.69	12.14	5.64	23.71	3.03	0.21	3.70

1985

SOURCE OF VARIATION	df	MEAN SQUARES NGL	TH	BL	SSHL	TOTL	BA	SSHA	TOTA
REPLICATES	1	0.35	2.47	241.52	0.13	253.09	14.34	0.01	14.91
WATER	1	3.87	12.51	0.46	19.51	28.48	1.82	0.74	0.24
CLIPPING	1	130.49***	12781.10***	7797.44**	6015.69***	27407.96**	301.65**	226.39***	1050.71**
WATERxCLIPPING	1	2.16	12.14	117.40	54.49	343.55	3.43	2.04	10.82
ERROR A	3	0.61	17.35	115.88	29.19	228.83	4.96	1.11	9.57
SPECIES	1	13.01**	43.01	2.10	168.71**	215.67*	0.20	6.33**	8.81*
WATERxSPECIES	1	1.89*	32.26	84.07	16.54	168.62*	11.24**	0.63	17.15*
CLIPPINGxSPECIES	1	0.24	2.88	6.82	128.53**	203.43*	1.24	4.83**	10.97*
WATERxCLIPPINGxSPECIES	1	0.51	4.25	33.04	3.85	54.87	4.99*	0.15	6.88
ERROR B	4	0.24	20.70	12.08	4.48	19.92	0.67	0.17	1.20
DATES	6	19.88***	158.72***	2067.50***	44.40***	2416.56***	88.47***	1.67***	97.43***
WATERxDATES	6	0.77***	15.04***	86.85***	25.91***	183.20***	6.44***	0.98***	11.40***
CLIPPINGxDATES	6	9.51***	504.91***	573.62***	232.39***	1273.82***	15.31***	8.75***	33.98***
SPECIESxDATES	6	2.31***	52.30***	53.01***	49.78***	156.96***	5.95***	1.88***	13.38***
WATERxCLIPPINGxDATES	6	0.26**	3.10	11.67	12.39***	31.31*	0.45	0.47***	1.19
WATERxSPECIESxDATES	6	0.37***	2.12	13.15	3.79	16.71	0.51	0.14	0.43
CLIPPINGxSPECIESxDATES	6	0.45***	2.44	10.56	7.18*	9.53	0.61	0.27**	0.91
WATERxCLIPPINGxSPECIESxDATES	6	0.21**	2.38	8.56	1.80	10.59	0.41	0.07	0.40
ERROR C	47	0.07	2.16	7.31	2.40	12.06	0.40	0.09	0.61

1986

SOURCE OF VARIATION	df	MEAN SQUARES							
		NGL	TH	BL	SSHL	TOTL	BA	SSHA	TOTA
REPLICATES	1	0.01	12.16	13.89	62.48	17.62	1.58	2.34	0.07
WATER	1	0.84	21.00	7.65	1.58	16.24	5.24	0.06	6.39
CLIPPING	1	14.33**	2137.13**	4144.73***	1024.39*	9291.32**	352.60***	38.55*	624.28**
WATERxCLIPPING	1	0.01	8.27	0.09	2.88	1.92	1.54	0.11	0.81
ERROR A	3	0.16	51.15	20.52	74.56	154.51	1.96	2.80	6.98
SPECIES	1	5.49*	15.63	26.83	51.51*	152.71*	4.84	1.93*	12.96*
WATERxSPECIES	1	0.01	141.01*	193.10**	68.11*	490.72**	18.86**	2.56*	35.41**
CLIPPINGxSPECIES	1	0.01	0.49	0.15	14.04	17.18	0.21	0.53	0.07
WATERxCLIPPINGxSPECIES	1	2.47	202.87*	457.13**	134.97**	1089.37***	27.99**	5.08**	56.98**
ERROR B	4	0.35	13.39	9.23	5.24	11.40	0.81	0.20	1.41
DATES	3	0.30	496.08***	178.72***	637.71***	876.75***	21.11***	24.02***	48.02***
WATERxDATES	3	1.84***	40.88**	177.71***	29.72	342.73***	9.69***	1.12	16.74***
CLIPPINGxDATES	3	4.68***	418.93***	619.95***	331.28***	1702.69***	36.52***	12.46***	82.40***
SPECIESxDATES	3	0.26	36.76*	14.13	40.03*	31.86	2.09*	1.51*	1.12
WATERxCLIPPINGxDATES	3	0.15	3.43	13.02	6.63	35.94	1.46	0.25	2.85
WATERxSPECIESxDATES	3	0.30	3.41	12.58	5.62	15.63	0.74	0.21	0.97
CLIPPINGxSPECIESxDATES	3	0.10	24.32	23.52	18.87	54.35	2.29**	0.70	3.32
WATERxCLIPPINGxSPECIESxDATES	2	0.40	27.90	24.10	20.16	87.40*	1.70*	0.76	3.86
ERROR C	23	0.22	8.82	9.87	12.00	23.90	0.50	0.45	1.24

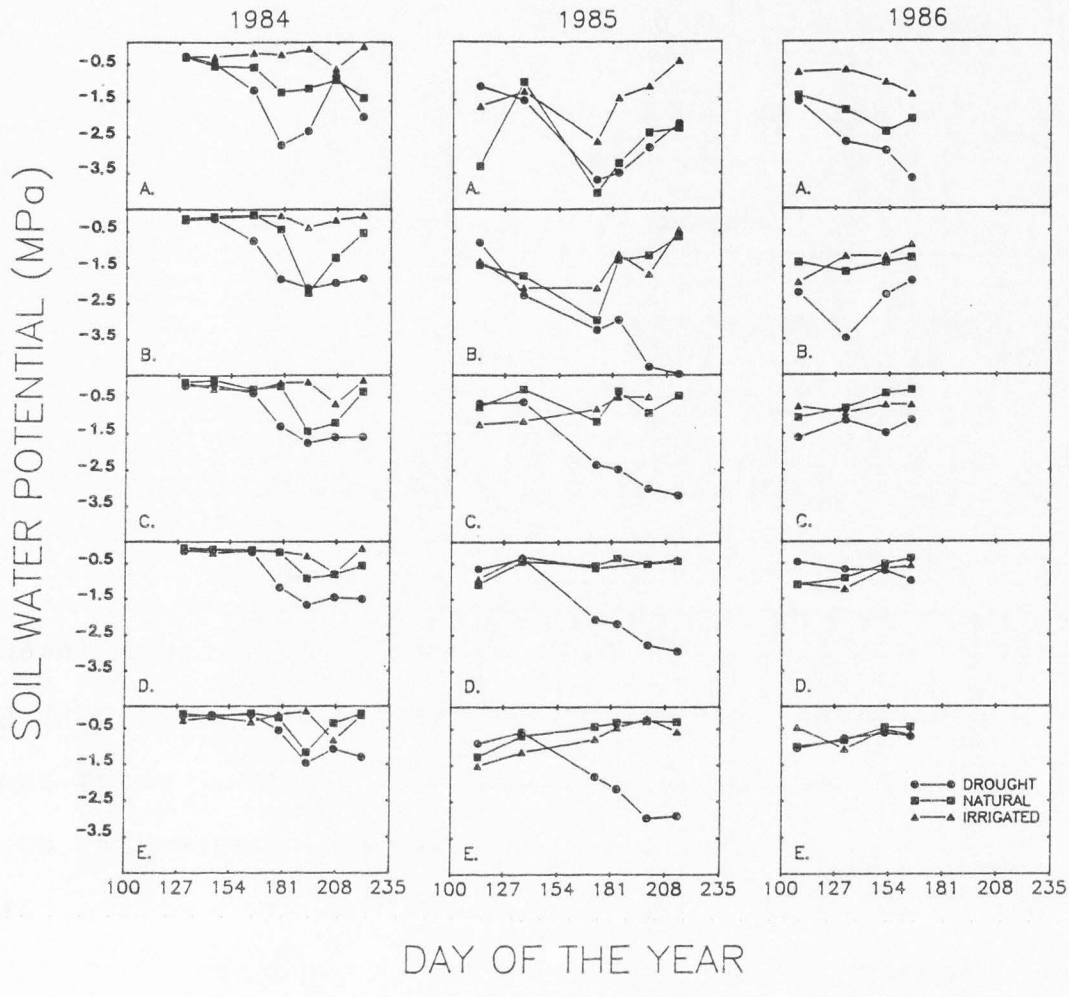


Fig. 24. Soil water potentials at 10 (A), 20 (B), 35 (C), 50 (D), and 80 (E) cm depths in the drought, natural and irrigated plots during the growing seasons of 1984-1986. Each symbol is the mean of 3 or 4 psychrometer observations. Values for 1984 are unpublished data from R.W. Brown.

Fig. 25. Frequency distribution of unclipped tillers (n=60) among phenological stages for A. desertorum (Agde) and A. spicatum (Agsp) in drought, natural or irrigated plots from 17 June through 25 Sept. 1984. Phenological stages are: 00 = vegetative, 10 = early reproductive, 20 = reproductive, 31-39 = increasing degrees of senescence, 40 = dead.

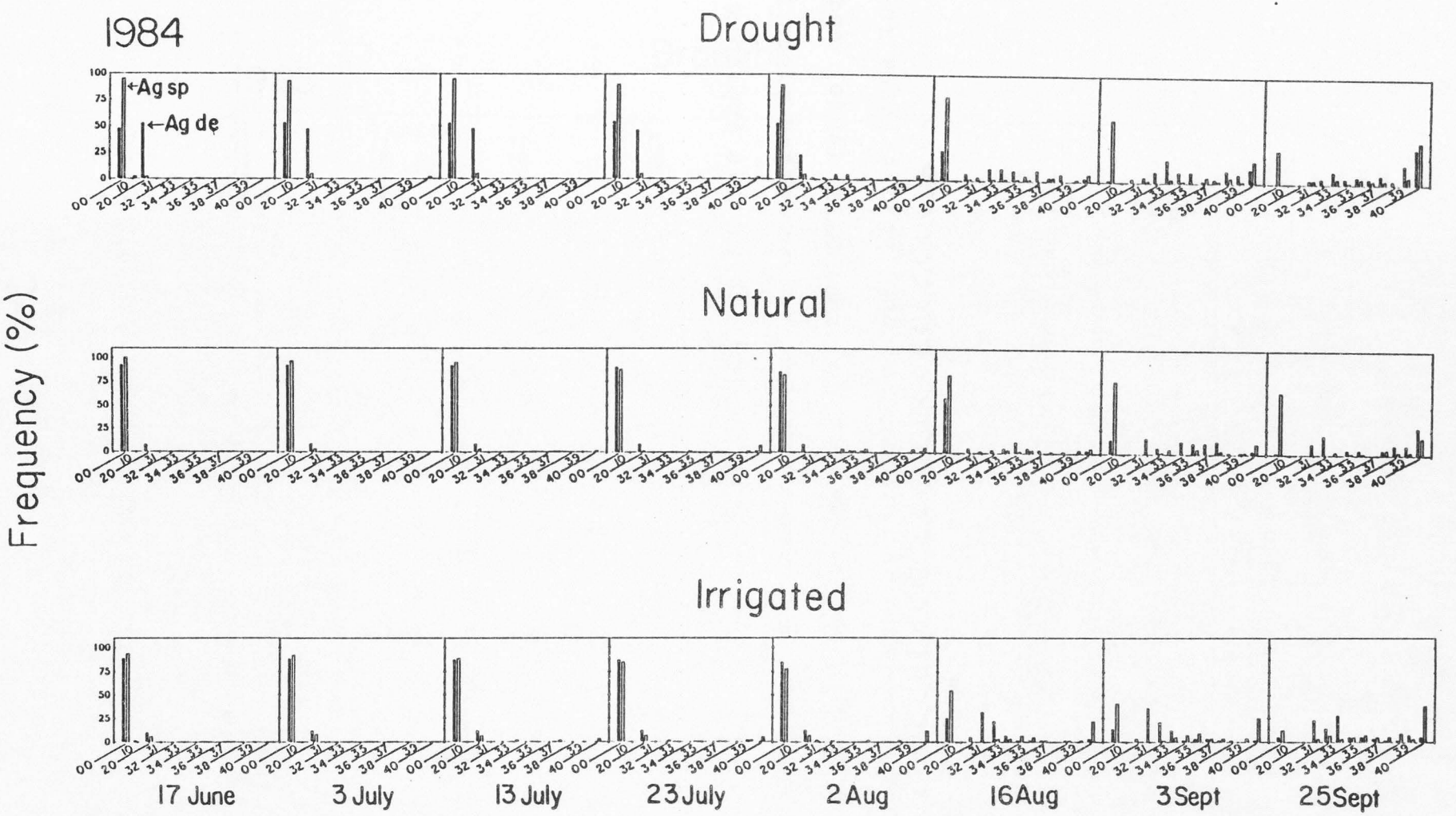
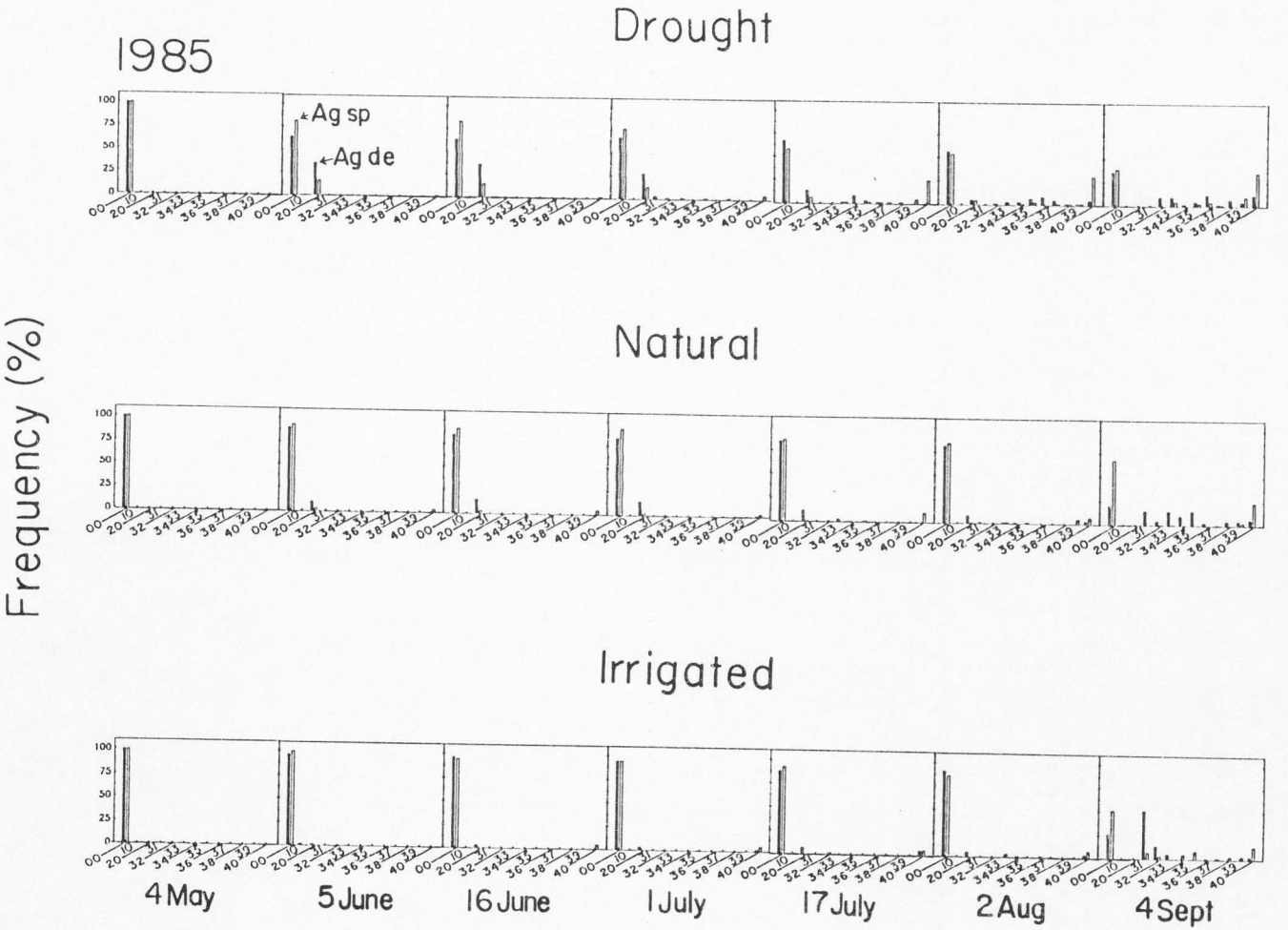

1984
Drought
←Ag sp
←Ag de
Natural
Irrigated
Frequency (%)
100
75
50
25
0
17 June
3 July
13 July
23 July
2 Aug
16 Aug
3 Sept
25 Sept

Fig. 26. Frequency distribution of unclipped tillers (n=60) among phenological stages for A. desertorum (Agde) and A. spicatum (Agsp) in drought, natural and irrigated plots from 4 May through 4 Sept. 1985. See Fig. 25 in this Appendix for a description of phenological stages.


1985
Drought
Ag sp
Ag de
Natural
Irrigated
Frequency (%)
100
75
50
25
0
4 May
5 June
16 June
1 July
17 July
2 Aug
4 Sept

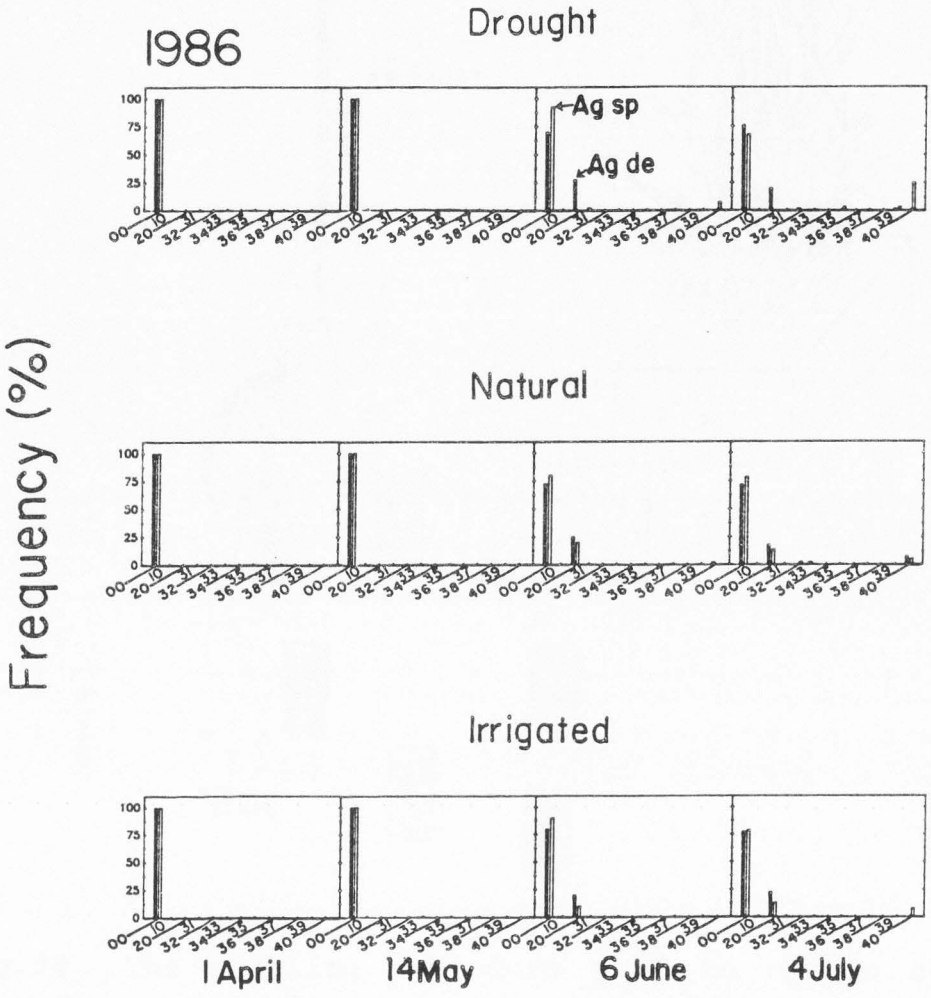


Fig. 27. Frequency distribution of unclipped tillers (n=60) among phenological stages for A. desertorum (Agde) and A. spicatum (Agsp) in drought, natural or irrigated plots from 1 April through 4 July 1986. See Fig. 25 in this Appendix for a description of phenological stages.

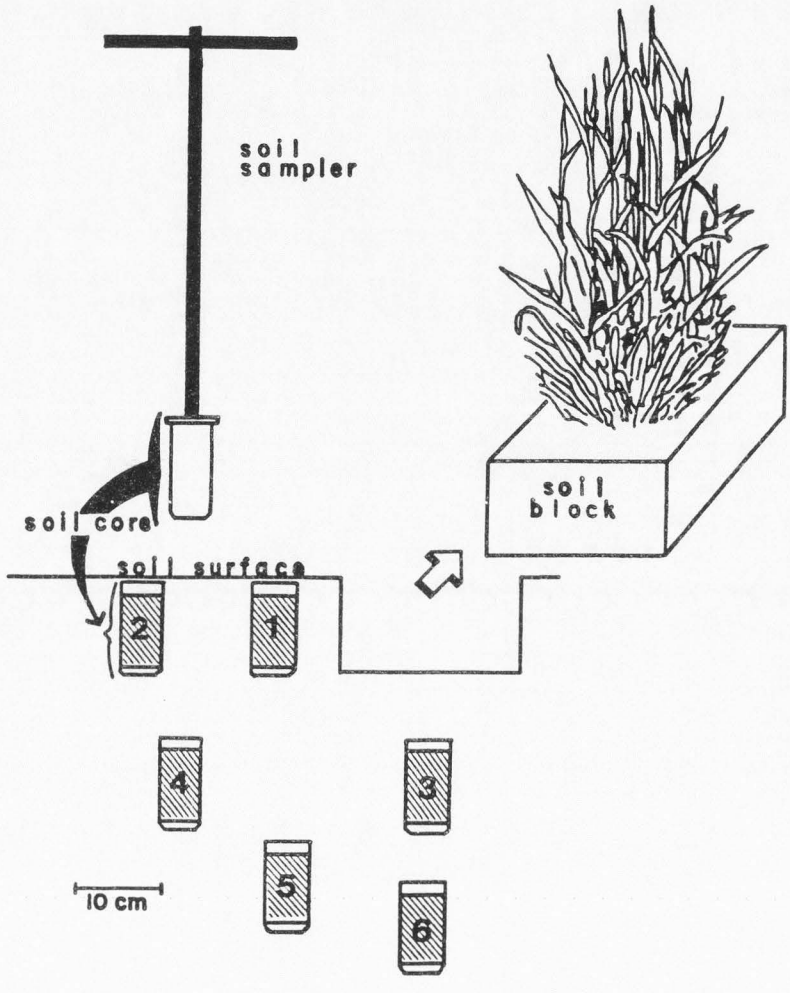


Fig.28. The sampling procedure used to obtain aboveground and belowground samples for biomass and TNC concentration determinations is illustrated. Root and crowns contained in a 20x20x10 cm soil block, and roots included in the striped portions (0.16 dm^3 volume) of soil cores numbered 1 through 6 were used for biomass determinations and TNC analysis. Samples 1 through 6 were collected in a direction between neighboring sagebrush and toward the healthiest neighbor grass plant of the same species. Aboveground plant parts were divided into current leaf blades and stem + sheaths prior to biomass and TNC measurements.

VITA

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